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Laboratoire des Reptiles et Amphibiens, Muséum national d'Histoire naturelle, 25 rue Cuvier, 75005 Paris, France. – Tel.: (33).(0)1.40.79.34.87. – Fax: (33).(0)1.40.79.34.88. – E-mail: dubois@mnhn.fr.

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Editorial

Alain DUBOIS

Laboratoire des Reptiles et Amphibiens,
Muséum national d'Histoire naturelle,
25 rue Cuvier, 75005 Paris, France

This issue of *Alytes* contains three papers that deal with the taxonomy and nomenclature of ranoid frogs, a fascinating research subject that still promises many novelties in the coming decades. Two of these papers include discussions of nomenclatural matters, that were written when the third edition of the *International Code of Zoological Nomenclature* (ANONYMOUS, 1985) was in force. Actually, this edition is still in force at the time of this publication, but for a few months only: in September 1999, the fourth edition of the *Code* (ANONYMOUS, 1999) was published, whose provisions are to replace those of the third edition as of 1 January 2000. Some of the nomenclatural discussions of these two papers will then become irrelevant. Thus, according to the new Article 16, after that date, any new species name will be nomenclaturally available only if "explicitly indicated as intentionally new" and accompanied in the original publication by the explicit fixation of a holotype or syntypes, and by reference to the collection of deposition of this or these specimen(s). These new rules are highly welcome, as they will limit seriously the risk of publication of "phantom names" as defined below in this issue by VENCES et al. (1999). Let us note however that they do not apply to names published before 1 January 2000.

The new edition contains other important changes regarding some articles of the *Code*, that will no doubt be discussed by zoologists worldwide in the coming years. One of them deserves particular attention: the new Article 23.9 introduces the concepts of "reversal of precedence", of "prevailing usage" and of "*nomen protectum*". This article states that, whenever two names are considered synonyms or homonyms, "prevailing usage" must be maintained when "the senior synonym or homonym has not been used as a valid name after 1899", and "the junior synonym or homonym has been used for a particular taxon, as its presumed valid name, in at least 25 works, published by at least 10 authors in the immediately preceding 50 years and encompassing a span of not less than 10 years". Had the word *available* been used instead of *valid* in this article, the latter would have raised no major problem and would have been welcomed virtually by all zoologists. But the use of the term *valid* opens the door for possible abuses and for future problems and discussions. It is no mystery for any experienced taxonomist that many names treated once as "invalid" because they were then considered junior subjective synonyms were later "resurrected" when this subjective synonymy was demonstrated to be wrong. The new article "moderates" the application of the Principle of Priority in this case, to replace it (without naming it) by a so-called "principle of usage". However, there is no doubt that, unlike priority, usage can be "deliberately rigged or manipulated" (DUBOIS, 1995b, 1997). A tendency already exists for some zoologists, when describing a new taxon, to coin a new name for it even if names are

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already available and may even be widely known but sometimes "hidden in synonymies" (for recent examples in amphibians, see e.g.: DUBOIS, 1995a, 1998, 1999a-b; DUBOIS & OHLER, 1995, 1998, 1999). The new Article 23.9 may be received by some authors as an encouragement for hasty and careless work, or even for deliberate omission of names published prior to 1900, in order to create "their" names. Ten years is a very short period in taxonomy indeed, and such poor nomenclatural actions may be quickly "validated" through this new article. This would not only, as some previous recent actions and statements, be an insult to the zoologists of the past (some of whom were at least as careful and competent as recent ones), and "to the thousands of authors who have followed the principle of priority (...) and thanks to whom stability has been reached for the very large majority of names" (DUBOIS, 1995c). More importantly, perhaps, this would be liable to strengthen the current progressive growth of a lax attitude of neglect or ignorance of the basic nomenclatural rules in zoology (see e.g. DUBOIS & OHLER, 1997, 1999), that might rather quickly lead to a chaotic situation in this field, as discussed below in this issue (DUBOIS, 1999b).

In view of these potential problems, the greatest attention will be paid, in the coming years, during the review process, to the nomenclatural aspect of papers describing new amphibian taxa submitted for publication to *Alytes*: such papers will be checked to provide all necessary information showing that a careful analysis of the situation has been carried out and that no earlier name is available for any such taxon. Hopefully, all other zoological journals worldwide will follow the same editorial policy.

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A review of the genus *Mantella* (Anura, Ranidae, Mantellinae): taxonomy, distribution and conservation of Malagasy poison frogs

Miguel VENCES *, Frank GLAW ** & Wolfgang BÖHME *

* Zoologisches Forschungsinstitut und Museum Alexander Koenig, Adenauerallee 160, 53113 Bonn, Germany

** Zoologische Staatssammlung, Münchenstr. 21, 81247 München, Germany

In this paper, 17 species of the genus *Mantella* are recognized and the genus is partitioned into six species groups which can be distinguished by combination of bioacoustic, morphological, osteological and coloration characters. The following species and species groups are recognized: *Mantella betsileo* group (*Mantella betsileo*, *Mantella viridis*, *Mantella expectata*, *Mantella* sp. 1, and one new species described herein); *Mantella laevigata* group (*Mantella laevigata*); *Mantella cowani* group (*Mantella cowani*, *Mantella baroni*, *Mantella* aff. *baroni*, *Mantella haraldmeieri*, *Mantella nigricans*); *Mantella bernhardi* group (*Mantella bernhardi*); *Mantella madagascariensis* group (*Mantella madagascariensis*, *Mantella pulchra*); *Mantella aurantiaca* group (*Mantella aurantiaca*, *Mantella crocea*, *Mantella milotympanum*). This partition is of rather high resolution, and some of the groups may also be regarded as superspecies or species complexes.

A detailed type re-examination showed that *M. madagascariensis* and *M. baroni* represent two different species which are very similar in dorsal coloration, but *M. madagascariensis* can be distinguished by some characters of ventral coloration (horseshoe marking on the throat, reddish color ventrally on femur) and morphology (large inner metatarsal tubercle) from *M. baroni*.

Specimens from Marojezy preserved in the Paris museum are catalogued as *M. cowani nigricans* and must therefore be considered as syntypes of this taxon. The syntype series is heterogeneous, also containing specimens of *M. laevigata*. The name *nigricans* is stabilized by designation of a lectotype corresponding to a *M. cowani* group form from Marojezy. The name *Mantella cowani nigricans* Guibé, 1978 is revalidated and raised to species rank as *Mantella nigricans*.

A big problem in *Mantella* systematics is that, in recent years, hobbyists increasingly tend to publish "phantom" scientific names without type designation which in several cases lead to involuntary but nomenclaturally available new nominal taxa. Two phantom names which must be considered as nomenclaturally available are *Mantella aurantiaca milotympanum* Staniszewski, 1996 and *Mantella aurantiaca rubra* Staniszewski, 1996. We consider the name *rubra* as synonym of *M. aurantiaca*, but preliminarily attribute specific status to *M. milotympanum*.

Lectotypes (in addition to *M. nigricans*) are designated for *M. cowani*, *M. aurantiaca*, *M. betsileo*, *Mantella attemsi* (synonym of *M. betsileo*), *M. aurantiaca rubra* (synonym of *M. aurantiaca*) and *M. milotympanum*.

(from published figure). Clarifications on types and type series are provided for several species.

We provide a key to the species of the genus *Mantella*, and describe and discuss their color variability. In several species, a large intraspecific color variability was recorded (*M. aff. baroni*, *M. nigricans*, *M. crocea*). A detailed review of all published *Mantella* localities and the corresponding voucher specimens results in updated distribution maps. Sympatric and syntopic occurrence was reliably only found in species from different species groups, the species within each group being allopatrically distributed. Future studies on contact and hybrid zones may demonstrate that some of the species recognized herein should possibly better be regarded as subspecies; however, for practical reasons, we here regard all taxa as species.

In an attempt to provide an estimate of the conservation status of each *Mantella* species, we combined data on distribution (maximum locality distance, number of known localities), habitat (primary forest restriction), trade intensity and attractiveness to the pet trade. We group the species in various classes, according to their potential vulnerability, and outline priorities of research needed to get a more reliable data basis for such estimates.

INTRODUCTION

The ranoid subfamily Mantellinae currently contains two genera, both endemic to Madagascar (GLAW & VENCES, 1994): the type genus *Mantella*, and the large and heterogeneous *Mantidactylus* with currently 63 species. *Mantella* are small, largely diurnal and often colorful frogs, which were named Malagasy (or Madagascan) poison frogs due to the presence of alkaloid toxins in their skin (e.g. DALY et al., 1996).

Accounts on the genus were published by GUIBÉ (1964, 1978) and BUSSE (1981). BLOMMERS-SCHLÖSSER & BLANC (1991) largely relied on BUSSE's revision which they complemented by detailed distribution maps. The description of four new species by PINTAK & BÖHME (1988, 1990), BUSSE & BÖHME (1992) and VENCES et al. (1994) demonstrated, however, that those accounts were far from being complete. While GUIBÉ (1978) listed only four species and one subspecies, GLAW & VENCES (1994) already accepted 13 different species.

One of the major problems in *Mantella* systematics has been weak morphological differentiation. Since early workers generally studied only preserved material, they had to rely largely on color pattern for species diagnoses. GUIBÉ (1964, 1978) and especially BUSSE (1981) considered single species (named *M. cowani* or *M. madagascariensis*, respectively) as highly variable in coloration, but they never proved this variability in specimens from a single locality (DALY et al., 1996). Without definite knowledge of intra- and interpopulational color variability, the attribution of type specimens of early names (*M. madagascariensis*, *M. cowani*, *M. baroni*, *M. pulchra*) largely depended on the subjective impression of the corresponding author, causing large confusion in the usage of these names in scientific and non-scientific literature.

In the following we report the main results on taxonomy, distribution and color variability of *Mantella* which were gathered in the framework of a comprehensive study of the genus. Contributions to the morphometry, osteology, tadpole morphology, reproduction, karyology, as well as bioacoustic and allozyme differentiation within *Mantella* are being published elsewhere. The aim of the present paper is mainly to clarify the taxonomy and nomenclature

of *Mantella* species as well as their distribution, in order to give a more stable basis for future investigations of these frogs. We divide the genus into phenetic species groups, and use our new scheme of *Mantella* systematics to discuss biogeographical subjects and to summarize conservation needs.

MATERIAL AND METHODS

SPECIMENS EXAMINED

The present review is mainly based on preserved material of the following collections: The Natural History Museum, London (BMNH); Field Museum of Natural History, Chicago (FMNH); Museum of Comparative Zoology, Cambridge (MCZ); Muséum National d'Histoire Naturelle, Paris (MNHN); Museo Regionale di Scienze Naturali, Torino (MRSN/MZUT); Naturhistorisches Museum Basel (NMB); Naturhistorisches Museum Wien (NMW); Transvaal Museum, Pretoria (TM); Zoölogisch Museum Amsterdam (ZMA); Museum für Naturkunde der Humboldt-Universität zu Berlin (ZMB); Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn (ZFMK). Specimens were examined in detail and their color patterns and morphology recorded. Locality and collector are generally literally given according to the corresponding catalogue. Abbreviations used are: CS, cleared and stained specimens; TE, tissue extracted for electrophoresis, specimens only partly preserved (generally liver extracted and two limbs amputated); NIL, specimens not individually labeled. The term "ex" is used in the sense of "formerly" to characterize old collection numbers.

LOCALITIES AND DISTRIBUTION MAPS

The examined material is the basis of the locality maps and the statements on color variability. Localities are numbered, the numbers corresponding to those in the respective distribution maps. A star behind the locality number marks the localities which were confirmed by FG (and partly by MV) in the field. The type locality, in the nomenclatural account on each taxon, is given in quotation marks literally as in the original description; additional discussions, when necessary, are provided in the *Comments* sections.

DESCRIPTION OF COLOR PATTERNS

Variation of color patterns is described in a standardized way and generally refers to live coloration of adult specimens. Terms which we use to refer to certain color elements are defined as follows: (1) dorsolateral color border: a sharp longitudinal border between the color of the flanks (darker) and the dorsum (lighter); (2) frenal stripe: a light longitudinal stripe along the upper lip; (3) rostral stripe: a light (yellowish, greenish or brownish) stripe running from anterior head tip and nostril above the eye to a point behind the eye;

(4) diamond marking: a central (dark) marking on the back of more or less distinct double-rhomboid shape; (5) flank blotches: light markings of varying extension which are located posterodorsally around the forelimb insertion and anterodorsally around the hindlimb insertion; they mostly can be seen as an extension of the dorsal humerus/femur color on the flanks; (6) flashmark: a sharply delimited, bright orange or red marking on the posterodorsal femur, knee hollow and ventral tibia which in some species can cover the ventral tibia nearly entirely; (7) horseshoe marking: a light (generally whitish blue) continuous marking on the throat, running more or less broadly along the lower lip and thus horseshoe-shaped. The terms femur, tibia, and tarsus, as used in the sections on coloration, do not refer to the skeletal elements but to the external coloration of the corresponding hindlimb sections.

MORPHOMETRY AND MORPHOLOGY

Measurements taken were: SVL: snout-vent length; HW: maximum head width; HL: head length, measured from snout tip to forelimb insertion (not to maxilla articulation); Eye: horizontal eye diameter; Tym: horizontal tympanum diameter; Eye-Ns: distance between eye and nostril; Ns-St: distance between nostril and snout tip; ForL: forelimb length; HaL: hand length; HiL: hindlimb length; FoTL: foot length including tarsus; FoL: foot length; ToL1: length of first toe; FW3: width of third finger just before terminal finger disk; DW3: width of terminal disk of third finger; IMTL, IMTH, IMTW: length, height and width of inner metatarsal tubercle. All measurements were made by the senior author with a precision calliper to the nearest 0.1 mm, except FW3, DW3, IMTL, IMTH, IMTW which were measured using a binocular with measuring device to the nearest 0.01 mm or, when no binocular was available, with a calliper to the nearest 0.1 mm. Original measurements in the present paper are only given for type specimens, but the size ranges and morphometric ratios in the species accounts refer to a total of about 400 measured specimens.

In the text, besides SVL, we use the abbreviations IMT for inner metatarsal tubercle, and TTA for tibiotarsal articulation. The size (SVL) is given as range of adult specimens, followed where possible by the range recorded in the males and females which could be reliably sexed. Since in many cases specimens could not be sexed with a sufficient reliability, known adult size range may be wider than that recorded in males and females separately.

DESCRIPTION OF CALLS

Detailed call descriptions will be published elsewhere; here we tentatively distinguish four different general call types: (1) double click calls are series of notes which each are composed of two emphasized and very short "metallic" clicks; (2) single click calls are series of notes which each are composed of one emphasized and very short "metallic" click; (3) trill calls are (irregularly or regularly repeated) notes composed of up to 10 short clicks; (4) chirp calls consist of (irregularly or regularly repeated) notes with a less "metallic" appearance than in click calls as used above (a note is often composed of 2-3 emphasized pulses).

SYNONYMIES

For each *Mantella* species, we present a synonymy and chresonymy (for the definition of the term chresonymy, see SMITH & SMITH, 1973), following the scheme used by DAVID & VOGEL (1996). The overwhelming number of publications in which at least one species of *Mantella* is mentioned makes it impossible to provide a complete chresonymy. Instead, we present a selection of references (partial chresonymy) which either (1) discuss intrageneric taxonomy and systematics, (2) provide original data for at least one species, (3) include pictures of at least one species, or (4) were published before GUIBÉ's (1964) revision of the genus (the latter, however, must be seen with reservation since it is often difficult to understand to which species the author actually referred). Page numbers are only given if necessary to locate a deviating name usage or a figure. Only publications which contain either original data or figures are listed in the chresonymies of the species. Exceptions are the works of GUIBÉ (1964, 1978), BUSSE (1981), BLOMMERS-SCHLÖSSER & BLANC (1991) and GLAW & VENCES (1992a, 1994), which are here considered as monographic accounts on the genus. All names used in these works are listed in the corresponding synonymies. Generally, taxa which were defined in a publication in a way that, according to present definition, they were in fact composed of several species, are listed as "partim-chresonyms" ("part.") in the chresonymies of each of these species (in the case of monographs) or of the species which were shown or explicitly meant (in the case of other papers). Nomenclatural validity of names is discussed according to the *International Code of Zoological Nomenclature* (ANONYMOUS, 1985; cited below as "the Code").

RESULTS

THE GENUS *MANTELLA**Definition of the genus*

Following the data of GUIBÉ (1978), BLOMMERS-SCHLÖSSER & BLANC (1991), BLOMMERS-SCHLÖSSER (1993), DALY et al. (1996), GLAW et al. (1998b), PINTAK et al. (1998), VENCES & KNIEL (1998) and VENCES et al. (1998, 1999a), the genus *Mantella* can be defined by the combination of the following characters:

(1) Eight presacral vertebrae; (2) vertebral centrae procoelous; (3) sacral diapophyses not enlarged; (4) atlantal cotyles widely separated; (5) three free distal tarsals; (6) six free distal carpals; (7) terminal phalanges slightly Y-shaped; (8) hyoid with anterolateral and posterolateral processes; (9) anterior processes of hyalia forming complete arch in some specimens of most or all species; (10) palatines present; (11) maxillary and premaxillary teeth absent; (12) vomer present; (13) dentigerous process of vomer (and thus vomerine teeth) absent; (14) squamosal with reduced zygomatic process; (15) frontoparietals anteriorly convex-shaped and separated along their whole length; (16) process of pars fascialis of maxilla reduced; (17) shoulder girdle firmisternal; (18) ossified sternum and omosternum present; (19) sternum

shorter than omosternum; (20) omosternum forked at its base; (21) complete ventral circum-marginal groove on terminal finger and toe expansions; (22) SVL of adults 18-31 mm; (23) tibiotarsal articulation reaching between forelimb insertion and nostril; (24) tympanum visible externally, mean tympanum/eye ratio 1/2 to 2/3; (25) lateral metatarsalia connected; (26) no webbing between fingers nor toes; (27) inner and outer metatarsal tubercle present; (28) no dorsal "scutes" on finger and toe tips; (29) karyotype $2n = 26$, with 5 pairs of large and 8 pairs of small chromosomes which are meta- or submetacentric; (30) tongue very slightly notched; (31) microphagous and myrmecophagous feeding; (32) skin alkaloids present; (33) long prey-capture jumps absent; (34) colorful pattern at least ventrally (black/blue, yellow or orange), often also dorsally; (35) activity largely diurnal; (36) calls consisting of short clicks, chirps or trills; (37) no strong mating amplexus; (38) eggs generally laid outside of the water; (39) eggs unpigmented; (40) tadpoles with horny beak and keratodont formula $1:2+2/3$ to $1:5+5/3$ (formula according to DUBOIS, 1995); (41) no tadpole transport; (42) no external gills in early larval stages; (43) egg clutches consisting of less than 200 eggs; (44) no externally prominent femoral glands as in many *Mantidactylus*, but granular thigh patches present (see also DALY et al., 1996), most distinct in males (exact structure of these patches will be subject to a forthcoming publication).

Character states 9, 11, 14, 30, 31, 32, 33 and 34 are, as far as known, not found in *Mantidactylus*, the second genus of the Mantellinae. They all can be considered as derived in *Mantella* (based on outgroup comparison with other ranid frogs, e.g. the Malagasy rhacophorines of the genus *Boophis*). However, states of characters 11, 13, 14, 16, 30, 32, 33, 34 and 35 are all part of a character complex related to microphagy (character 31), which reduces their value as independent characters for the assessment of phylogenetic relationships (see VENCES et al., 1998). In fact, most of them are also found in the Dendrobatidae which, too, are microphagous but clearly differ from *Mantella* in other characters (different states in characters 5, 6, 7, 18, 20, 28, 29, 30, 40, 41 and 42; for references, see VENCES et al., 1998). Apomorphic states supporting the status of *Mantella* as a monophyletic (holophyletic) group within the Mantellinae are thus the microphagy character complex (see above) and the hyoid structure (character 9).

Etymology of the generic name

The genus *Mantella* was erected by BOULENGER (1882) to accommodate the species *betsileo*, *madagascariensis* and *ebenau*; in an addendum he described the new species *cowanii*. The type species is *Mantella betsileo*, as designated by LIEM (1970). No etymology was given in the original description of the genus. The generic name is most probably a diminutive of *mantis* (Classical Greek *mantis*, prophet) which was used with the meaning "treefrog" in the sense of a weather prophet by HESYCHIUS. This meaning of *mantis* is included in several Greek-German dictionaries (e.g. PAPE, 1888) but was not found in Greek-French or Greek-English dictionaries (see GLAW & VENCES, 1994: 400). The term *mantis* was often used for generic anuran names; BOULENGER himself erected in 1895 the genus *Mantidactylus* for several Madagascan frogs which today are included together with *Mantella* in the Mantellinae.

A second etymology for *Mantella*, however, cannot be totally excluded. One of the early subjects of BOULENGER's studies were dinosaur fossils found in Belgium, which belonged to the genus *Iguanodon*. The first *Iguanodon* fossils had been found by an English doctor,

G. MANTELL, and his wife, and were subsequently described as *Iguanodon mantelli* (see BULTYNCK, 1987). Still less probable is a derivation from the Italian word *mantella* (cloak) which is sometimes used to describe animal (mammal) color patterns.

DEFINITION OF SPECIES GROUPS

Although several authors have stressed similarities between selected *Mantella* species and erected species groups within the genus (GLAW & VENCES, 1994, ZIMMERMANN, 1996a; STANISZEWSKI, 1996), no comprehensive attempt has so far been published to partition the whole genus into such groups, and to explicitly list the characters distinguishing them. We here divide the genus into six phenetic species groups, a subdivision of rather high resolution; in fact, some groups could also be characterized as superspecies or species complexes. The differential characters between species groups are summarized in tab. 1.

Mantella betsileo group (contains: *Mantella betsileo*, *M* sp 1, *M. viridis*, *M. expectata*, and one new species described herein). – This group is characterized by the combination of several characters which, however, are each also present in at least one other species group: double click call (also in *M. laevigata*), horseshoe marking (also in several other groups), frenal stripe (also in *M. crocea* and some *M. madagascariensis*), hindlimbs ventrally black without orange and red (also in *M. laevigata* and *M. nigricans*)

Mantella laevigata group (contains: *Mantella laevigata*). – The classification of *Mantella laevigata* in a separate species group is clearly justified by its unique habits (partly arboreal, tree hole breeding, single eggs) and its distinctly enlarged finger tips. It is the only species with a double click call which lacks a horseshoe marking

Mantella cowani group (contains *Mantella baroni*, *M* aff. *baroni*, *M. cowani*, *M. nigricans*, *M. haraldmeieri*). A group characterized by light (mostly yellow or red) flank blotches of variable extension (also found in the *M. madagascariensis* group and in *M. bernhardi*) and single click calls (exclusive to this group).

Mantella bernhardi group (contains: *Mantella bernhardi*) Classification of *M. bernhardi* in a separate species group is mainly based on its relevant allozyme differentiation (VENCES et al., 1999b) and its trill calls

Mantella madagascariensis group (contains: *Mantella madagascariensis*, *M. pulchra*). – The species included in this group are mainly characterized by a very large IMT (see diagnosis of *M. pulchra* in GÜLF, 1964, 1978). Light flank blotches of varying extension, horseshoe markings and flashmarks are present. Calls, as far as known, are chirp calls.

Mantella aurantiaca group (contains: *Mantella aurantiaca*, *M. crocea*, *M. milotympanum*). – Species of this group are characterized by a rather stout body shape, distinct flashmarks and a chirp call. In contrast to species of the *M. madagascariensis* group, there are no flank blotches and the IMT is smaller. Two species (*M. aurantiaca*, *M. milotympanum*) are characterized by a largely uniform yellow to red dorsal and ventral coloration. *M. crocea* is included in this group since specimens with color pattern intermediate between *M. crocea* and *M. milotympanum* are known (GLAW & VENCES, 1998), and juvenile coloration of *M. crocea* and *M. aurantiaca* is very similar (personal observation). The close relationships between the

Table 1. Differential characters between *Mantella* species groups. Not all characters have been ascertained in all species of the groups. See *Definition of species groups* section for more information. Sternum shape is given according to VENCES et al. (1999a). IMT, inner metatarsal tubercle.

Character	<i>Mantella betsileo</i> group	<i>Mantella laevigata</i> group	<i>Mantella cowani</i> group	<i>Mantella bernhardi</i> group	<i>Mantella madagascariensis</i> group	<i>Mantella aurantiaca</i> group
Call	mostly double click, series	double click, series	single click, series	trill, mostly no series	chirp, series	chirp, mostly no series ¹
Sternum	forked	forked	unforked	unforked	forked	forked
Horseshoe marking	present	absent	absent	present	present	present/absent
Frenal stripe	present	absent	absent	absent	absent (present) ²	present/absent
Flank blotches	absent	absent	large/small	small	large	absent
Orange/red ventral color on hindlimbs	absent	absent	present (absent) ³	present	present	present
Habitat	terrestrial	partly arboreal	terrestrial	terrestrial	terrestrial	terrestrial
Eggs laid as	clumps	single eggs	clumps	clumps	clumps	clumps
Egg feeding of tadpoles	absent	present	absent	absent	absent	absent
IMT	small	small	small	small	large	small

¹ Only ascertained in *M. aurantiaca*, *M. crocea* calls are also chirp calls (personal observation), but notes may be arranged more often in series than in *M. aurantiaca*.

² A frenal stripe may be present in certain specimens of the "variable" morph of *M. madagascariensis*.

³ Orange-red ventral color on hindlimbs is present in all species of the *M. cowani* group except *M. nigricans*.

species of the *M. aurantiaca* group were supported by chromosome morphology (PINTAK et al., 1998) and by studies on allozyme variation (VENCES et al., 1999b). ZIMMERMANN (1996) also mentioned a *M. aurantiaca* group which included *M. aurantiaca* and *M. crocea*.

SPECIES ACCOUNTS

In the following, we list *Mantella* species separately for each species group; within the groups, species are arranged alphabetically. Photographs of living specimens of all species are shown in fig. 1-3, dorsal and ventral views of holotypes and lectotypes (all photographed 1992-1999) in fig. 4-5, and variation of ventral pattern in fig. 6-8. Distribution maps are shown in fig. 9.

Mantella betsileo group

Mantella betsileo (Grandidier, 1872)

Dendrobates betsileo Grandidier, 1872 Name-bearing type lectotype, by present designation, MNHN 1895 278, sex unknown due to bad state of preservation, SVL 19.0 mm *Type locality* "Pays des Betsileos" according to original description and MNHN catalogue - *Other types* paralectotype, following present lectotype designation, MNHN 1895 279 - *Etymology*: named after the type locality, the region Betsileo.

Mantella betsileo BOULENGER, 1882, 1888, VAILLANT, 1885, WERNER, 1901, MOCQUARD, 1909, METHEN & HEWITT, 1913, MILLOT & GUIBÉ, 1964, 1978, LIEM, 1970, BACHMANN & BLOMMERS-SCHLÖSSER, 1975, BLOMMERS-SCHLÖSSER, 1978, 1979a, MEIER, 1980 (part, p. 353, third figure from above), 1986 (Abb. 3); BUSSE, 1981 (part.; see *M. haraldmeieri*); PINTAK, 1990, BLOMMERS-SCHLÖSSER & BLANC, 1991 (part.), 1993 (plate 19 101), ANDREONE, 1992 (pl. III fig. 3-4), GLAW & VENCES, 1992a (part., see localities), 1992b (fig. p. 29), 1994 (part., see localities), ZIMMERMANN & ZIMMERMANN, 1997 (fig. 5 17) GARRAFFO et al., 1993, HERRMANN, 1993 (fig.), KUCHLING, 1993; BARTLETT, 1995 (fig. p. 26), HENKEL & SCHMIDT, 1995 (fig. p. 50), CARISSIMI-PRJORI, 1995 (fig. p. 42); VENCES et al., 1996, 1998, DALY et al., 1996, STANISZEWSKI, 1997a (fig.), 1997b (fig.); LARSEN, 1997; PINTAK et al., 1998, VENCES & KNIEL, 1998.

Dendrobates ebenau Boettger, 1880 Name-bearing type lectotype, by designation of MERTENS (1967: 44), SMF 7323 (ex 1141, 1a), adult female. - *Type locality*: "insula Nossi Be", according to original description - *Other types*: possibly one paralectotype, FMNH 18236 or 18237 (see MARX, 1958, and comment below). *Etymology*: named after C. EBENAU who provided the type material.

Dendrobates ebenau MOCQUARD, 1909 (syn. *betsileo*), MERTENS, 1922 (syn. *betsileo*), MERTENS, 1967 (syn. *betsileo*).

Dendrobates ebenau: GUIBÉ, 1964, 1978 (syn. *betsileo*); BUSSE, 1981 (syn. *betsileo*); BLOMMERS-SCHLÖSSER & BLANC, 1991 (syn. *betsileo*), GLAW & VENCES, 1994 (syn. *betsileo*: p. 411).

Mantella ebenau BOULENGER, 1882, WERNER, 1901, METHEN & HEWITT, 1913 (syn. *betsileo*).

Mantella attemsi Werner, 1901 Name-bearing type lectotype, by present designation, NMW 20837, female, SVL 25.6 mm *Type locality* uncertain, but (in original description) was speculated to be probably "Madagascar oder Nossi-Be" - *Other types* paralectotype, following present lectotype designation, ZMB 16588 - *Etymology*: named after C. ATTEMIS who provided the type specimens from Zanzibar.

Mantella Attemsi MOCQUARD, 1909

Mantella attemsi: GUIBÉ, 1964, 1978 (syn. *betsileo*), BUSSE, 1981 (syn. *betsileo*), BLOMMERS-SCHLÖSSER & BLANC, 1991 (syn. *betsileo*), GLAW & VENCES, 1994 (syn. *betsileo*: p. 412); HAUPI et al., 1994 (syn. *betsileo*).

Identity DALY et al. (1996) were concerned about the fact that the type locality of *M. betsileo* (see below) is outside the known range of the species. They questioned whether the name is currently correctly applied. A re-examination of the types (see below) leads us to

conclude that they (1) cannot be conspecific with any species having red or orange ventral color on the hindlimbs, (2) are morphologically different from *M. laevigata* and *M. nigricans*, and (3) are smaller than *M. viridis*, *M. sp. 1* and *M. expectata*. It seems therefore likely that the name is currently (e.g. GLAW & VENCES, 1994) correctly applied.

Comments. – (1) The taxon *betsileo* was originally based on the syntypes MNHN 1895.278-279. The lectotype MNHN 1895.278 (SVL 19.0 mm; sex unknown) is larger and in slightly better state of preservation. The paralectotype MNHN 1895.279 is probably a subadult specimen (SVL 15.7 mm). In both types, coloration has become a contrastless, nearly uniform brown. The dorsolateral coloration border mentioned in the original description cannot be unequivocally recognized. Since the hindlimbs were folded in both specimens, the pattern is less faded on the posteriorly directed (ventral) part of the tibia which was not exposed to light. Here, a distinct light crossband can be recognized, as is typical for species of the *M. betsileo* group (and for *M. laevigata* and *M. nigricans*). Based on this character it can be excluded that the types are conspecific with *Mantella* species having red or orange color ventrally on the hindlimbs. (2) The type locality of *M. betsileo* is a large region in central Madagascar. Up to now, no *Mantella betsileo* specimens are known to have been collected in the eastern forests south of Nosy Boraha. As discussed by DALY et al. (1996), the travel routes of GRANDIDIER are rather well documented. Maybe, the types were not collected in the eastern Betsileo forests but in western Betsileo, where the occurrence of *M. betsileo* seems more probable due to the existence of several localities in western Madagascar. It also cannot be excluded that the type locality is wrong. (3) According to the original description (BOETTGER, 1880: 281), *Dendrobates ebenaui* was based on two syntypes, a male and a female. However, in his 1892 catalogue, BOETTGER (1892: 21) mentioned “numerous specimens” (“Zahlr. Ste”) of this species from Nossibé, kept in the Frankfurt Museum under number SMF 1141.1a: presumably these specimens included the two original syntypes and several other non-type specimens. MERTENS (1922: 166) stated that the “Typus” of this species was bearing the number SMF 1141.1a, but since this number was used by BOETTGER (1892) as a collective number for a series, this mention cannot be considered as a lectotype designation under article 47 (b) of the Code. Designation of an individual specimen, SMF 7323, as lectotype of this species, was made by MERTENS (1967: 44). Thus, only one paralectotype exists. It might be one of the two FMNH “paratypes” listed by MARX (1958), which were presumably part of the series mentioned by BOETTGER (1892). Further clarification of the status of these two specimens is necessary. (4) The description of *Mantella attemsi* was based on two specimens (WERNER, 1901), corresponding to the specimens NMW 20837 and ZMB 16588. Both are today in a rather bad state of preservation. Color patterns are largely faded, only the dorsolateral color border is still recognizable. In the lectotype NMW 20837, a few ventral color patterns (light vermiculated markings on the posterior venter) are still faintly recognizable. The paralectotype ZMB 16588 is most probably a male.

Material examined. Difficulty of identification of specimens as *M. betsileo* is enhanced by the existence of a very similar, undescribed species (*M. sp. 1*, see below). Since this species is generally larger than *M. betsileo*, size was one of the major diagnostic characters for preserved specimens with faded coloration. However, we cannot totally exclude that some specimens may be wrongly identified and in fact be subadults of *M. sp. 1*. In parentheses, we give SVL for most specimens.

The following specimens can clearly be assigned to *M. betsileo*: BMNH 84.11.3.4 (Nosy Be, purch. from “Linnaea”), BMNH 86.2.25.25-28 (Nosy Be, “Senckenberg Museum”, N.L., SVL 23.7 mm,

20.7 mm, 22.2 mm, 23.3 mm), BMNH 1909 10 19 21 (Nosy Be; P. KREFFT); BMNH 1926 10.27 4-7 (Antongil forest, Maroantsetra, purch ROSENBERG; NIL; largest female 25.3 mm); BMNH 1952 1.1.55-56 (Rantabe, Antongil bay, Maroantsetra; coll C S WEBB; female 55 25.7 mm); ZFMK 17604-9 (Maroantsetra; leg. H MEIER I 1976); ZFMK 27680 (Maroantsetra, leg. H. MLIER X 1979); ZFMK 28867-8 (Nossi-Bé; through Linnaea 1886, originally Museum Göttingen); ZFMK 46004 (Nosy Boraha [Ile Ste. Marie]; leg. F W HENKEL II.1987, CS); ZFMK 46781-3 (Nosy Be Loucoube, leg. R. SEIPP IV 1987); ZFMK 47007 (Nosy Bé Loucoubé; leg. F W. HENKEL & J SAMEIT II 1987); ZFMK 47218 (Sahafary, leg. F. GLAW XI 1987); ZFMK 47289 (Nosy Boraha [Ile Ste. Marie], leg. H. MEIER XI 1987); ZFMK 48257-8 (Nosy Bé Loucoubé, leg. W SCHMIDT 1987); ZFMK 52744 (Nosy Boraha [Ile Ste. Marie]; leg. F. GLAW & M VENCES III.1991); ZFMK 52745 (Nosy Bé, leg. F GLAW & M. VENCES III 1991); ZFMK 51818 (Nosy Boraha [Ile Ste. Marie], leg. F. W. HENKEL et al 1988-89); ZFMK 53708-10 (Nosy Bé, leg. F GLAW & J MULLER II.1992, juveniles); ZFMK 59978-9 (Kirindy, leg. F GLAW I.1995); ZFMK 62685-7 (locality unknown, CS); ZFMK 62689-96 (locality unknown, TE); ZFMK 62688 (Nosy Be, leg. K. SCHMIDT; TE); MRSN A0064.1-4 (Maroantsetra; leg. F ANDREONE 23 IV.1990); MRSN A0068 1-2 (Kirindy, leg. R. NINCHERI 22 XII 1992)

The following specimens are assigned to *M. betsileo* based on size, general appearance and morphometric characters such as relative hindlimb length. BMNH 94 2 27.21 (Madagascar, coll LAST, purch GERARD; pattern totally faded), BMNH 1930.7 1 54-57 (valley 3/4 miles W of Ampoza, 15 miles E of Ankazoabo, SW Madagascar, pres. WHITE, rather small specimens, NIL) MNHN 1884 603-4 (Nossi Bé, SVL 25 mm [603], 21 mm [604]), MNHN 1885 34-7 (locality unknown, SVL 21 mm [34], 18 mm [35], 20 mm [36], 18 mm [37]), MNHN 1885 48 (Nossi Bé), MNHN 1895 278 9 (lectotype and paratype, Pays des Betsileos), MNHN 1896 435-6 (Madagascar, "acquis de l'Institut Linnaea", color totally faded, SVL 24 mm [435, female?], 23 mm [436]), MNHN 1900 15 (Pays Mahafaly, au Sud, with remark "male Joly", SVL 20 mm), MNHN 1929 225 (source de Namoroko [Ambongo]; juv. ? SVL 16 mm), MNHN 1953 129, MNHN 1991 1795 [originally 129a] (forêt d'Manjaba; TTA reaches eye center [1795], SVL 25 mm [129], 24 mm [1795]), few ventral markings, absent on breast [1795]), MNHN 1953.131, MNHN 1991 1796 [originally 131a] (Bas Manongarivo; SVL 17 mm [131], 16 mm [1796]), MNHN 1953.130, MNHN 1953 133 (locality unknown, SVL 23 mm [130, 133]), MNHN 1953 134 (Nossi-Bé Lokobe, Manjoky, juv., SVL 13 mm), MNHN 1962 895 (Namoroka, grotte de Bemahara, R. PALLIAN IX 52, TTA reaches eye center, SVL 22 mm), MNHN 1962 896-7 (Anove, forêt littorale, A. DOMERGUE I 1961, TTA reaches eye center [896, 897], SVL 21 mm [896], 22 mm [897]), MNHN 1976 200-2 (Nosy Komba, SVL 21.1 mm [200], 19.7 mm [201], 19.3 mm [203]), TM 9858-67 (Eastern Region, Madagascar, coll HIRSCHHELL-CHAUVIN)

The following MNHN specimens with unknown locality are here assigned to *M. betsileo* only based on their size which is given in parentheses MNHN 1976 181 2 (SVL 22 3 mm [181], 22 0 mm [182]), MNHN 1976 187 (SVL 22 2 mm), MNHN 1976 206 (SVL 19 5 mm), MNHN 1976 222-3 (SVL 20 9 mm [222], 17 6 mm [223]), MNHN 1976 225 (SVL 22 1 mm), MNHN 1976 227 (SVL 22 1 mm), MNHN 1976 230 (SVL 22 8 mm)

The status of two specimens is not sufficiently clarified. They have enlarged disks on fingers and toes and thus resemble *M. laevigata*. MNHN 1953 132, MNHN 1991 1797 [originally 132a] (Isaratanana, TTA reaches between tympanum and eye [132], SVL 25 mm [132], 20 5 mm [1797])

Distribution Except the type locality "Pays des Betsileos", all known localities are located in lowlands (altitude between 0 and ca. 500 m), generally near the coast. Also, all east coast localities are in an area north of Betsileo (see DALY et al., 1996: 19). Confirmation of the type locality would therefore be important.

The species is common along the east coast in the Maroantsetra region and on Nosy Boraha, and in the Sambirano region, it also occurs along the west coast. Localities are as follows. [1*] Nosy Boraha (<10 m altitude); [2*] Voloina (GLAW & VENCES, observations in 1991), [3] Maroantsetra, [4] Rantabe, [5*] Sahafary; [6] Anove, [7] Antanambaobe, and Ambavala near Sandrakatsy in the Mananara reserve (DALY et al., 1996: 100-200 m altitude); [8] Farakaraina near Maroantsetra (DALY et al., 1996, 30 m altitude), [9*] Nosy Be; [10*]

Nosy Komba; [11*] Benavony (F. GLAW & J. MÜLLER, observations in 1992); [12] Ankify (village near ferry docks N Ambanja, personal communication of W. B. LOVE); [13] Manongarivo; [14] Tsaratanana (SCHIMMENTI, personal communication); [15*] Kirindy (Amborom-potsy, see KUCHLING, 1993); [16] Namoroka; [17] Tsingy de Bemaraha (SCHIMMENTI, personal communication); [18] Mahafaly (?); [19] Ampoza (not traced and therefore not included in the distribution map).

The Mahafaly locality (MNHN 1900 15) in the very arid South-Western Region needs confirmation but seems corroborated by the specimens from Ampoza in SW-Madagascar, and is therefore accepted here in a preliminary way. Specimens from the Anosy mountains in southern Madagascar identified as *M. betsileo* by BUSSE (1981) in fact belong to *M. haraldmeieri* (see below). MILLOT & GUIBÉ (1951) mentioned the species from the "forêt de Bevia" near Fort Dauphin, but we could not find voucher specimens for this locality in the Paris Museum. Also HENKEL & SCHMIDT (1995) gave no vouchers for their locality Tolagnaro. We consider these localities in need of confirmation, and do not accept them here.

We did not find voucher specimens for seven additional localities which were listed by BLOMMERS-SCHLÖSSER & BLANC (1991). Of these, Nosy Mangabe probably was based on BUSSE (1981: 29) who stated that specimens of *M. laevigata* collected by H. MEIER (on Nosy Mangabe) lived parapatrically or sympatrically with *M. betsileo*. We did not find *M. betsileo* on Nosy Mangabe, and the locality thus needs confirmation. The population from Montagne des Français (near Antsiranana) is here referred to *M. viridis* (see below), and those from Morondava, Androatsabo and Tongahybe to *M. sp. 1* (see below). Baly probably refers to Tongahybe, since in the Paris Museum catalogue the additional remark "Baly Ouest" is given for the corresponding specimens (see section on *M. sp. 1*). We did not find vouchers from Andranoboka in the Paris Museum and therefore consider this locality in need of confirmation.

Diagnosis (1) *Morphology*. A small, relatively slender *Mantella*. SVL, males 18-21 mm, females 19-26 mm. TTA mostly reaching eye center. Terminal disks of fingers and toes expanded. Tympanum/eye ratio generally 1/2 to 3/5. IMT medium sized (ratio width/length about 2/3). (2) *Dorsal color and pattern*. Dorsal head surface and dorsum yellowish to orange or light brown, mostly with a diamond marking and a sharp dorsolateral color border to the largely black flanks. White frenal stripe present. Limbs brown to grey, with at least one dark brown crossband on femur, tibia and tarsus. Iris with light pigment in its upper part. (3) *Ventral color and pattern*. Black with blue markings of different size and extension often showing vermiculated patterns and fusing with each other. Breast region generally with light markings, smaller than those on posterior venter. Distinct horseshoe marking present, of larger extension in males than in females, and sometimes including a central stripe.

Mantella expectata Busse & Bohme, 1992

Mantella expectata Busse & Bohme, 1992. *Name-bearing type* holotype by original designation (BUSSE & BOHME, 1992: 58), ZFMK 53540 male, SVL 23.4 mm. *Type locality* "20 km southeast of Tolara (=Tulear), W-Madagascar" according to original description. *Other types* paratypes ZFMK 53541-2, ZFMK 59095-8 and four (lost) additional paratypes (see comment below). *Etymology* derived from Latin *expectare* (to await), rediscovery of this species was awaited during several years after MEIER (1986) first published a picture of it.

Mantella expectata GLAW & VENCES, 1992a, 1994, HERRMANN, 1993 (fig.), LE BERRE, 1993 (fig. p. 20), HENKEL & SCHMIDT, 1995 (fig. p. 52), BARTLETT, 1995 (fig. p. 26), VENCES et al., 1996, DALY et al., 1996, STANISZEWSKI, 1996 (plate p. 18), 1997a (fig. p. 16), 1997b (fig.), 1998a (fig.); VENCES & KNIEL, 1998

Other chresonyms:

Pictured in MEIER (1986 fig. 8) as "Eine noch unbekannte *Mantella*-Form".

Comment. - In the original description (BUSSE & BÖHME, 1992), beside the catalogued specimens ZFMK 53541-2, "eight living specimens which will be incorporated in the ZFMK collection later" were also designated as paratypes. Of these captive stock, only four specimens were eventually preserved and catalogued as ZFMK 59095-8; the remaining four paratypes must be considered as lost.

Material examined - ZFMK 53540 (SE Tulear; leg. G. GOTTLIBE II 1992, holotype); ZFMK 53541-2 (SE Tulear; leg. G. GOTTLIBE II 1992, paratypes), ZFMK 59095-8 (SE Tulear; through pet trade, paratypes), ZFMK 62713-5, ZFMK 62789 (locality unknown; TE), ZFMK 62716-7 (locality unknown, CS)

Distribution - Known from: [1] the type locality, 20 km SE of Toliara; [2] the area around Morondava, based on a picture made by a German development aid worker and published by MEIER (1986); [3] the Isalo massif (altitude ca. 800 m), based on a personal communication of A. PEYRIERAS and on DALY et al. (1996). The locality Mandena in south-eastern Madagascar, given by GLAW & VENCES (1994), was based on an erroneous information of G. HALLMANN and was corrected by VENCES et al. (1996).

Diagnosis. (1) *Morphology*: A medium-sized, stout *Mantella* SVL 20-26 mm. TTA sometimes reaching only the tympanum, but generally reaching the eye center. Terminal disks of fingers and toes expanded. Mean tympanum/eye ratio nearly 3/5. IMT medium sized (ratio width/length slightly more than 2/3). - (2) *Dorsal color and pattern*: Head and dorsum dirty yellow to lemon yellow with a sharp dorsolateral color border to the black flanks. Limbs grey to bright metallic blue. A thin bluish white frenal stripe present. Iris with light pigment in its upper part. - (3) *Ventral color and pattern*: Black with irregularly shaped blue markings which can fuse to form a blue-black marbling. Blue markings present on the breast. Throat largely blue, as a very extended horseshoe marking.

***Mantella manery* n. sp.**

Mantella sp. GLAW & VENCES, 1994, VENCES et al., 1996

Mantella "marojezyi" [conditional name], STANISZEWSKI, 1996, 1997a, 1997b (e.g. p. 16-18)

Mantella "marojezyi" [conditional name], STANISZEWSKI, 1997b (p. 61)

Mantella "marojezyi" [conditional name], LARSEN, 1997.

Name-bearing type - A single specimen of this species was preserved and deposited in the herpetological collection of the Zoological Institute of the Antananarivo University, Madagascar (leg. F. GLAW, N. RABIBISOA & O. RAMILISON, 27.III.1994) and is here designated as holotype. The following description is based on color slides of this specimen.

Type locality - Reserve Naturelle Intégrale Marojezy, near Camp 1, ca. 300 m altitude

Other types. - None.

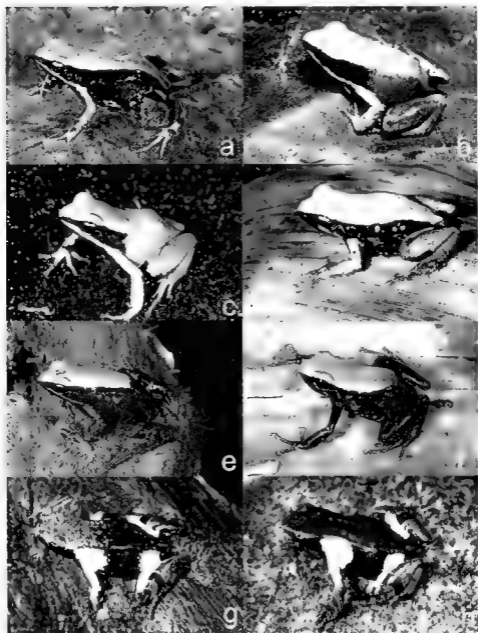


Fig 1 - Photographs of *Mantella* species. (a) *M. betsileo* from Nosy Be (specimen not preserved), 1992. (b) *M. sp. 1* from Ankarana (specimen not preserved), 1995. (c) *M. varidis* specimen without locality data (not preserved), 1995. (d) *M. eximata* specimen without locality data (not preserved), 1995. (e) *M. maneri* from Marojejy (holotype deposited in the herpetological collection of the Antananarivo University), 1994. (f) *M. laevigata* from Marojejy (specimen not preserved), 1995. (g-h) *M. nigricans* from Marojejy with and without greenish dorsal color patterns, 1995.

Identity. – Color patterns of this species differ from the remaining species of the *M. betsileo* group. Its occurrence in rainforest also differs from most other species of the group (except *M. betsileo*). It was considered a distinct species by GLAW & VENCES (1994). Unfortunately, no specimen of this form was available for detailed examination, as the only preserved specimen is stored in the herpetological collection of the University of Antananarivo. Until present, we thought that the description of this species should wait until new material was collected, and new data on its variation, calls, ecology and osteology became available. However, several hobbyist authors (e.g., STANISZEWSKI, 1996; LARSEN, 1997) have made reference to this form as “*Mantella marojezyi*”, “*Mantella marojezi*” or “*Mantella marojez*”, providing diagnoses which were entirely based on our previously published data. All authors who previously used these names wrote them in quotation marks; these usages thus must be seen as conditional names which are not nomenclaturally available according to article 15 of the *Code*. However, it can be expected that sooner or later the name will be used without quotation marks in any of the increasingly published hobbyist accounts on *Mantella* (see *Discussion* below), accompanied by a diagnosis, and will thus become valid. We therefore prefer to name the form by a formal preliminary description, designating the specimen stored in the Antananarivo collection as holotype. Our preliminary account should be complemented as soon as the holotype (currently not available to us) is examined in detail, and new field observations are made.

Etymology. Derived from the Malagasy verb *manery* (to force, forced), here used as an invariable substantive standing in apposition to the generic name. We were forced to describe and name this form in a preliminary way to avoid it being named without proper diagnosis in a hobbyist publication.

Distribution. – Only known from the type locality: [1*] Marojezy massif, near Camp 1.

Diagnosis. – The new species is a member of the *M. betsileo* group based on the presence of a horseshoe marking, frenal stripe, dorsolateral color border, and lack of orange/red color ventrally on the hindlimbs. It differs from all species of that group by the rounded light ventral spots (generally at least partly vermiculated in the other species of the group), the brownish posterior dorsum (of same color as anterior dorsum in the other species) and the dark brown dorsal color of fore- and hindlimbs (lighter in the other species). It further differs from *M. betsileo* and *M. sp. 1* by the greenish rather than brown dorsum; from *M. viridis* by the entirely dark brown flanks; and from *M. expectata* by the lack of bluish dorsal color on the dorsal surface of the limbs and the lesser extent of the light ventral spots and markings. (1)

Morphology of the holotype. Unknown, estimated SVL 25 mm. (2) *Dorsal color and pattern of the holotype*. Head and anterior part of dorsum yellowish green. Posterior part of dorsum and flanks dark brown. Sharp dorsolateral color border present anteriorly. The yellowish green dorsal color posteriorly ending straight (not semicircularly) and not covering the posterior part of the dorsum. A thin, light, partly interrupted frenal stripe present. Limbs dark brown with a very fine, irregular black dotting. Two dark crossbands on the hindlimb. Iris with light pigment in its upper part. See also color pictures in GLAW & VENCES (1994) and VENCES et al. (1996). (3) *Ventral color and pattern of the holotype*. Black with a relatively large number of small, regularly rounded blue markings which become smaller anteriorly. Horseshoe marking present.

Mantella sp. 1

Mantella n. sp. 3: CLARK, 1994

Chresonyms

Mantella betsileo: BLOMMERS-SCHLÖSSER & BLANC, 1991 (part.), GLAW & VENCES, 1992a (part., see localities), 1994 (part.; see localities)

Mantella cf. *betsileo*: VENCES et al., 1996.

Identity VENCES et al. (1996) first mentioned the presence of this form in Ankarana, based on the observations of J. KÖHLER. R. NUSSBAUM (personal communication) found it in the spiny desert of southern Madagascar and considered it as a species distinct from *M. betsileo*.

Comment No scientific name is currently disponible for this form. Formal description of this species will be the subject of a forthcoming paper

Material examined - ZFMK 61238-41 and ZFMK 62197-9 (Ankarana; leg. J. STEINBRECHER 1995, 61241· CS) Several MNHN specimens can also be referred to this species MNHN 1973.484-96 (Androatsalo), MNHN 1973 497 (Tongahybe [Baly-Ouest]); MNHN 1973 498 (Androatsalo), MNHN 1976 214-8 (Morondava; SVL 26.4 mm [214], 23.3 mm [215], 26.1 mm [216], 21.7 mm [217], 22 mm [218]) The specimens MNHN 1973 217-8 may also belong to *M. betsileo* which is known from Kirindy near Morondava (KUCHLING, 1993, GLAW & VENCES, 1994). Due to the large size of the specimens MNHN 1976.214 and MNHN 1976 216, we here refer the whole series to *M. sp. 1* We also refer to the species in a preliminary way a BMNH series: BMNH 74 10 29 1 4 (Mohambo, purch. M. BOUCARD, NIL, four females, SVL 26.5 mm, 25.9 mm, 25.4 mm, 21.0 mm, no light spots in thorax region)

Several other MNHN specimens with unknown localities may be referred to *M. sp. 1* based on their large size: MNHN 1976 183-6 (SVL 23.2 mm [183], 24.6 mm [184], 26.6 mm [185], 26.9 mm [186]); MNHN 1976 188 (SVL 23.6 mm), MNHN 1976 191 (SVL 24.2 mm), MNHN 1976 193 (SVL 27.3 mm); MNHN 1976.194 (SVL 25.1 mm), MNHN 1976 197 (SVL 24.5 mm), MNHN 1976 198 (SVL 26.4 mm), MNHN 1976 199 (SVL 27.1 mm)

Distribution [1] Ankarana; [2] Tongahybe; [3] Morondava, [4] Androatsalo (Androatsabo according to BLOMMERS-SCHLÖSSER & BLANC, 1991); [5] Mohambo (locality not traced and not included in map) According to NUSSBAUM (personal communication, see also CLARK 1994), large populations of this species occur in the spiny desert of south-western Madagascar.

Diagnosis - (1) **Morphology**. A large, rather stout *Mantella* SVL 22-30 mm, males 25 mm, females 29-30 mm. TTA reaching the posterior eye margin in small specimens (males), between forelimb insertion and tympanum in large females. Terminal disks of fingers and toes slightly expanded. Mean tympanum/eye ratio nearly 3/5. IMT medium sized (ratio width/length about 2/3). (2) **Dorsal color and pattern** Dorsal head surface and dorsum yellowish to light brown, mostly without diamond marking. Sharp dorsolateral color border anteriorly present. Flanks black, with fiery red color extending posteriorly. White frenal stripe present. Limbs brown to red-brown, with at least one dark brown crossband on femur, tibia and tarsus. Iris with light pigment in its upper part. - (3) **Ventral color and pattern**: Black with blue markings, of different size and extension but often showing vermiculated patterns and fusing with each other. Breast region generally without or with only very small light markings. Distinct horseshoe marking present, sometimes including a central stripe.

Mantella viridis Pintak & Böhme, 1988

Mantella viridis Pintak & Böhme, 1988. *Name-bearing type*: holotype by original designation (PINTAK & BÖHME, 1988: 120), ZFMK 47900, female, SVL 30.3 mm. - *Type locality*: "südlich Antseranana (= Diego Suarez), Nord-Madagaskar", according to original description. *Other types*: 11 (lost) paratypes (see comment below). - *Etymology*: derived from Latin *viridis* (green).

Mantella viridis: PINTAK, 1990, OLIVETTI, 1990 (fig.); BLOMMERS-SCHLOSSER & BLANC, 1991 (p. 274), ZIMMERMANN, 1992, GARRAFFO et al., 1993, ANDREONE, 1992 (plate III fig. 5-6), GLAW & VENCES, 1992a, 1994, HERRMANN, 1993 (fig.); LE BERRE, 1993 (fig. p. 20), ZIMMERMANN & ZIMMERMANN, 1994, BARTLETT, 1995 (fig. p. 17), HENKEL & SCHMIDT, 1995 (fig. p. 57), CARISSIMI-PRIORI, 1995 (fig. p. 43); VENCES et al., 1996, 1998; DALY et al., 1996, 1997a; STANISZEWSKI, 1997b (fig. p. 6), LARSEN, 1997; PINTAK et al., 1998; VENCES & KNIEL, 1998.

Mantella spec.: VAN TOMME, 1988 (fig. 2)

Other chresonyms:

Mantella betsileo: BUSSE, 1981 (part.); BLOMMERS-SCHLOSSER & BLANC, 1991 (part.), GLAW & VENCES, 1992a (part.; see localities), 1994 (part.; see localities)

Mantella expectata: STANISZEWSKI, 1997a (fig. p. 12).

Comment - In the original description (PINTAK & BÖHME, 1988), 11 living, uncatalogued specimens (four males and seven females, with same locality data as holotype) were designated as paratypes. No specimens of this captive stock were eventually preserved and catalogued; all paratypes must therefore be considered as lost.

Material examined: ZFMK 47900 (according to catalogue Mige d'Ambre, S of Diego [Antseranana], leg. D. BRETZ 1987, holotype), ZFMK 48038-53 (Antseranana [Diego Suarez]; leg. H. MEJER III 1988, 48048: CS), ZFMK 62708-9 (locality unknown, CS); ZFMK 62710-2 (locality unknown, TE); MRSN A416 (locality unknown; through the pet trade)

Three specimens (MNHN 1976 211-3, Montagne des Français) are also referred to *M. viridis* based on their locality, size and relative hindlimb length. They clearly cannot be attributed to *M. betsileo* as in the MNHN catalogue, but due to the faded colors we cannot completely exclude their belonging to *M. sp. 1*. MNHN 1992.4820 (locality unknown) is here also referred to *M. viridis* based on size and relative hindlimb length, although color patterns are not recognizable any more.

Distribution. Only known from the northern tip of Madagascar. The published type locality is south of Antseranana. The only reliable localities known are: [1] 13 km south of Antseranana (DALY et al., 1996); [2*] Montagne des Français (GLAW & VENCES, 1994; ca. 100-300 m altitude), south of Antseranana. ZFMK specimens with the locality "Antseranana" were most probably collected in the Montagne des Français. ANDREONE (1992) showed pictures of *Mantella viridis* from "area of Montagne d'Ambre National Park" (plate III fig. 5-6), but previously stated (p. 423) that he had not observed the species in nature and that locality information was based on PINTAK & BÖHME (1988). Most probably the species is not present in the Montagne d'Ambre National Park since recent surveys failed to find it (RAEWORTHY & NUSSBAUM, 1994; GLAW & VENCES, 1994).

Diagnosis (1) *Morphology*: A large, rather stout *Mantella*. SVL, males 22-25 mm, females 27-30 mm. TTA reaching the eye center in many specimens (mostly males), but only the forelimb insertion in large females. Terminal disks of fingers and toes expanded. Mean tympanum/eye ratio about 2/3. IMT medium sized (ratio width/length slightly less than 2/3).

(2) *Dorsal color and pattern*: Head, dorsum and largest (posterior) part of the flanks light green to yellowish. Anterior part of the flanks black, this color reaching in many specimens to a point around the forelimb insertion. A sharp dorsolateral color border present in this area.

Distinct, white to light green frenal stripe present. Color of limbs generally similar to dorsum, without a dark crossband, but hindlimbs with a metallic blue shade in some specimens. Iris with light pigment in its upper part. (3) – *Ventral color and pattern*: Black with bluish white markings decreasing in size from posteriorly to anteriorly, generally absent on the breast. Markings of irregular shape, often vermiculate and fusing with each other. Distinct horseshoe marking present on the throat.

Mantella laevigata group

Mantella laevigata Methuen & Hewitt, 1913

Mantella laevigata Methuen & Hewitt, 1913. *Name-bearing type*: holotype by original designation (METHUEN & HEWITT, 1913: 58), TM 10074 (ex 1214), sex unknown, SVL 22.5 mm. *Type locality*: "Folohy", according to original description and TM catalogue. *Other types*: six paratypes according to original description (ex 1212, 1215-9), TM 10085-8, TM 10090 and MCZ 10815 (see comment below). *Etymology*: derived from Latin *laevigare* (to make smooth).

Mantella laevigata GUIBÉ, 1964 (syn. *cowani*), 1978 (syn. *cowani*); BUSSE, 1981; MEIER, 1986; PINTAK, 1990; BLOMMERS-SCHLÖSSER & BLANC, 1991; ANDREONE, 1992 (plate IV fig. 1-2); GLAW & VENCES, 1992a, b, 1994; GARRAFFO et al., 1993; HERRMANN, 1993 (fig.), LE BERRE, 1993 (fig. p. 20), HFNKEL & SCHMIDT, 1995 (fig. p. 54), BARTLITT, 1995 (fig. p. 24), DALY et al., 1996; STANISZEWSKI, 1997a (fig.), 1997b (fig.), 1998a (fig.), LARSEN, 1997; GLAW et al., 1998a; PINTAK et al., 1998; VENCES et al., 1998; VENCES & KNIEL, 1998.

Other chrysonyms:

Mantella cowani: GUIBÉ, 1964 (part), 1978 (part).

Mantella madagascariensis: BLOMMERS-SCHLÖSSER & BLANC, 1991 (part) included in syntype series of subspecies *M. m. nigricans*, locality Marojezy, same applies to BUSSE, 1981, and GLAW & VENCES, 1992a, 1994).

Placed in MEIER (1980: fig. p. 353 below) as "Bisher nicht eindeutig einzuordnende *Mantella*-Art".

Comments. - (1) The holotype is in good state of preservation. The pattern is largely faded but still recognizable on head and anterior dorsum. A few of the light ventral spots are still recognizable; they are small and rounded. The paratypes TM 10085-6 are in a rather bad state of preservation; the pattern contrast is largely faded, and the ventral pattern is not recognizable. TM 10088 and 10090 are also in bad state of preservation with faded pattern, but they can clearly be assigned to *M. laevigata* by their broad finger disks. TM 10087 is in good state of preservation, pattern contrast is weak, but both dorsal and ventral (small rounded spots) pattern is still recognizable. - (2) Seemingly, the type locality "Folohy forest" does not exist any more; its location was traced by BLOMMERS-SCHLÖSSER & BLANC (1991) immediately north of Toamasina (Tamatave), and we follow this placement in our distribution maps. (3) Barbour & Loveridge (1929) mentioned the existence of one "syntype" in the TM and one in the MCZ (MCZ 10815). However, the original description (a) clearly stated that it was based on "seven examples", listed as "1212, 1214-1219" and (b) separately mentioned specimen 1214 once more, as "type". Although not explicitly stated, this infers the existence of one holotype (ex 1214, today TM 10074); we consider all additional specimens listed in the original description as paratypes. MCZ 10815 is almost certainly the specimen formerly numbered TM 10089, which was exchanged with MCZ, according to the TM catalogue, on

8 VII.1925. (4) Whereas the locality of the holotype and of the paratypes TM 10087-8 and MCZ 10815 is Fohohy, that of the paratypes TM 10085-6 and 10090 is only "E Madagascar", according to the TM catalogue.

Material examined. TM 10074 (Fohohy, Eastern Madagascar; coll. by HERSCHELL-CHAUVIN, 1911, holotype), TM 10085-6 and 10090 (Eastern Madagascar resp. East region, Malagasy Republic; coll. HERSCHELL-CHAUVIN, 1912, paratypes), TM 10087-8 (Fohohy, E-Madagascar; coll. HERSCHELL-CHAUVIN, 1912, paratypes); BMNH 1952.11 53-54 (Mangabe island, Antongil bay, coll. C. S. WEBB, NIL), MNHN 1973.534-40 (Marojezy, 300 m, paralectotypes of *M. nigricans*); MNHN 1973.542-7 (Marojezy, 300 m, paralectotypes of *M. nigricans*), MNHN 1973.549 (locality unknown, paralectotype of *M. nigricans*), MNHN 1973 557 8 (Marojezy, 600 m, paralectotypes of *M. nigricans*); two juvenile specimens of the MNHN collection most probably also belong to *M. laevigata* MNHN 1973 517 (Marojezy 300 m, SVL 12.3 mm, paralectotype of *M. nigricans*), MNHN 1973 548 (Marojezy 300 m, SVL 12 1 mm, paralectotype of *M. nigricans*); ZFMK 19298 (Maroantsetra, leg. H. MEIER 1976), ZFMK 48660 (Nosy Mangabe, leg. R. ZOBEL VI 1988); ZFMK 52747-51 (Nosy Mangabé; leg. F. GLAW & M. VENCES III 1991; 52749 CS); ZFMK 59911 (Marojezy Camp 1; leg. F. GLAW & O. RAMILISON II 1995), ZFMK 59912 (Marojezy Camp 2, leg. F. GLAW & O. RAMILISON II 1995; juvenile), ZFMK 59913-4 (Marojezy Camp 3, leg. F. GLAW & O. RAMILISON II 1995), ZFMK 62786-8 (locality unknown, TE), MRSN A0065.1-3 (Nosy Mangabe, leg. F. ANDREONE 24 IV 1990); MRSN A1826 (Tsararano Chain Camp 1, leg. F. ANDREONE 4 XII 1996), MRSN A1827, MRSN A1828 1-2 (Tsararano Chain, Camp 2, leg. F. ANDREONE 13-14.XII.1996).

Distribution. - [1] Type locality Fohohy. Recent localities from the East and North-East are. [2*] the small island Nosy Mangabe (100-300 m altitude); [3] the Tsararano chain (700 m altitude); [4*] the Marojezy massif (300-700 m altitude). Two additional localities from the northern part of the Eastern Region are found in DALY et al. (1996): [5] Ambodimanga and Varary, both in the Mananara reserve (ca. 100 m altitude). The locality Maroantsetra (based on ZFMK 19298, see BUSSÉ, 1981) does almost certainly not refer to the town Maroantsetra itself but to a nearby locality (most probably Nosy Mangabe) and is therefore not accepted here.

Diagnosis. - (1) *Morphology:* A medium sized to large *Mantella* with a generally very slender appearance. Terminal disks of fingers and toes largely expanded. SVL 22-29 mm. TTA reaching generally the eye center and slightly beyond the eye in some specimens. Tympanum/eye ratio between 1/2 and 3/5. IMT medium-sized (ratio width/length about 3/5)

(2) *Dorsal color and pattern:* Head and anterior part of dorsum covered by a sharply delimited yellow mark, posteriorly either ending semicircularly or prolonged as a pointed triangle to the cloacal region, with a sharp dorsolateral color border to the black flanks and sides of head. Variation in shape of dorsal yellow mark not corresponding to sexual dimorphism. Limbs deep black (exceptionally copper brownish). Hands and finger tips often with blue spots. No frenal stripe, but single yellowish spots sometimes present under the eyes. No flashmarks. Iris completely black without light pigment. - (3) *Ventral color and pattern:* Venter and limbs black with small, rounded, bluish or bluish-grey spots. Throat generally completely black without pattern (few light spots sometimes present). No red, orange or yellow pattern on hindlegs.

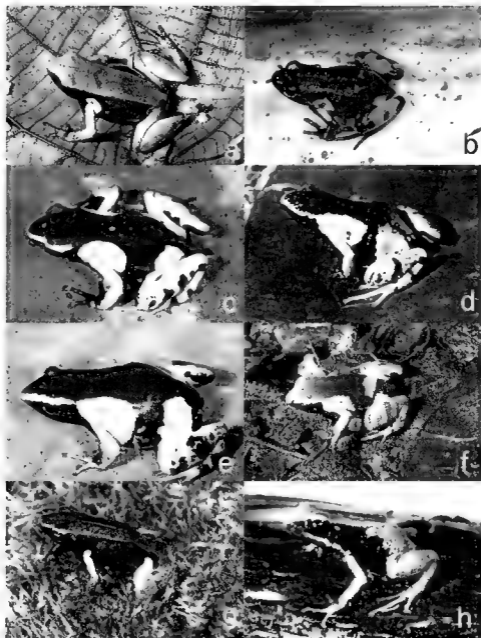


Fig 2. Photographs of *Mantella* species: (a) *M. baraldmayeri* from Nahampoana 1991 (b) *M. conanti* specimen without locality data (not preserved) 1994 (c) *M. baroni*, specimen without locality data (not preserved, but belonging to the same series as ZI MK 62718-75) 1997, (d) *M. all. baroni* from Andringitra (ZMA 6754), photograph taken from BLOMMERS-ST. HOUSSER & BLANC (1993), (e) *M. madagascanensis* specimen without locality data (not preserved, but belonging to the same series as ZI MK 62732-41), 1997, (f) *M. pulchra* specimen without locality data (not preserved), 1994, (g) *M. lewinbarthi* from near Tolongoma (holotype ZI MK 57164), 1994 (h) *M. crocea*, specimen without locality data (ZI-MK 52746), 1991

Mantella cowani group**Mantella baroni** Boulenger, 1888

Mantella Baroni Boulenger, 1888 *Name-bearing type* holotype by monotypy, BMNH 1947 2 7 19 (ex 84 12 22 50), male (according to the original description), SVL 27.2 mm *Type locality* not specified in the original description, "Madagascar" without further specifications according to the BMNH catalogue.

- *Etymology* named after the collector of the type, Reverend P. BARON

Mantella Baroni: MOCQUARD, 1909.

Mantella baroni WERNER, 1901, METHUEN & HEWITT 1913, PARKER, 1925, GUIBÉ, 1964, 1978 (syn *cowani*), BUSSE, 1981 (syn *madagascariensis*), BLOMMERS-SCHLÖSSER & BLANC, 1991 (syn *madagascariensis*); GLAW & VENCES, 1994 (syn. *madagascariensis*, p. 412); DALY et al., 1996, 1997b, PINTAK et al., 1998, VENCES et al., 1998, VENCES & KNIEL, 1998, STANISZEWSKI, 1998a (fig.)

Phrynomantis maculatus Thomodont, 1889 - *Name bearing type*, lectotype (designated by GLAW & VENCES, 1994), MNHN 1991 2845 (ex 6807a), sex unknown, SVL 27.0 mm. - *Type locality*, "Île de La Reunion" according to original description (probably erroneous, see comment below) *Other types* paralectotypes MNHN 1991 2846 (ex 6807b), MNHN 1991 2847 (ex 6807c) and MNHN 6807 *Etymology* derived from Latin *maculatus* (spotted)

Phrynomantis maculatus GUIBÉ, 1964, 1978 (syn *cowani*), BUSSE, 1981 (syn *madagascariensis*), BLOMMERS-SCHLÖSSER & BLANC, 1991 (syn. *madagascariensis*); GLAW & VENCES, 1994 (syn. *madagascariensis*; p. 413)

Other chrysonyms:

Mantella cowani, GUIBÉ, 1964, 1978 (part), MATZ, 1975 (fig. 1), MEIER, 1975 (fig. 1-2), MEIER, 1980 (fig. p. 352), OBERLE, 1981 (pl. 29), LE BERRE, 1993 (part, outer fig. p. 21)

Mantella madagascariensis BELTELSCHIESS & BEUTELSCHIESS, 1987, PINTAK, 1990 (part), OLIVETTI, 1990 (fig.), BLOMMERS-SCHLÖSSER & BLANC, 1991 (part), ANDREONE, 1992, GLAW & VENCES, 1992b (fig. p. 28), ZIMMERMANN & ZIMMERMANN, 1992 (fig. 5 21), GARRAFFO et al., 1993, CLARK, 1994 (fig. p. 10 below), VENCES et al., 1994 (fig. p. 390), GLAW & VENCES, 1994 (part), BARTLETT, 1995 (fig. p. 18 below right); HENKEL & SCHMIDT, 1995 (fig. p. 55), CARISSIMI-PRIORI, 1995 (fig. p. 42); STANISZEWSKI, 1996 (plate p. 16-17); 1997a (fig. p. 12), 1997b (fig.), ZIMMERMANN, 1996b (fig. 14)

Mantella madagascariensis sensu stricto: GLAW & VENCES, 1992a (part; see localities)

Mantella madagascariensis madagascariensis BUSSE, 1981 (part), MEIER, 1986 (fig. 6), VAN TOMME, 1988 (fig. 5-6); ANDREONE & GAVETTI, 1993 (p. 105).

Identity - BUSSE (1981) defined *M. madagascariensis* as a very variable species containing several junior synonyms, including *M. baroni*. One main problem with this definition was the bad state of preservation of the *M. madagascariensis* types (see below) which made reliable attribution of this name to any specific morph impossible. Recent studies have shown that many of the forms previously summarized under the name *M. madagascariensis* do in fact belong to separate well-defined, valid species (GLAW & VENCES, 1994). Two morphs (here named A and B) remained without an unequivocal definition. morph A, figured on plate 61 in GLAW & VENCES (1994), was considered as *M. madagascariensis*, whereas the "variable" morph B, figured on plates 58-59 in GLAW & VENCES (1994), was considered as *M. "loppet"* in a preliminary way. GLAW & VENCES (1994) mentioned that morph A corresponds to the type of *M. baroni* which they listed as synonym of *M. madagascariensis*. DALY et al. (1996), referring to this definition, argued that *M. baroni* should be revaluated as a valid name (for morph A), whereas the name *madagascariensis* should be seen as "nomen dubium" due to the bad state of the type specimens.

We here follow these conclusions as far as the definition of morph A as *Mantella baroni* is concerned. *M. madagascariensis*, however, is not "unidentifiable" (DALY et al., 1996); a new, detailed examination of the lectotype of that taxon showed that it corresponds to morph B (see corresponding section).

Comments - (1) The holotype of *M. baroni* is in rather bad state of preservation, but the relevant color patterns can still be recognized. (2) According to BLOMMERS-SCHLÖSSER & BLANC (1991), the number BMNH 1947.2.7 19 defines "syntypes" of *M. baroni*; however, BOULENGER (1888) in his original description mentioned explicitly "a single male specimen". We found no indications on the existence of types other than a single holotype in the BMNH collection and catalogue. The specimens ZFMK 28770-28772 cannot be seen as *M. baroni* "paratypes" as was suspected by BUSSE (1981); their collecting data agree with those of the series BMNH 95.7.4.34-6 and 96.12.2.28-31, but not with those of the holotype. (3) The type locality of *Phrynomantis maculatus*, according to the original description, is "Île de La Réunion". BUSSE (1981) first gave the locality "Nosy Cumba-Nosy Be" without providing additional information nor his source of information. This locality was subsequently also given by BLOMMERS-SCHLÖSSER & BLANC (1991) but was questioned by GLAW & VENCES (1994). According to A. OHLER (in litteris, 1997), a second MNHN catalogue informs that the specimens were supplied by the "Com. scientifique de Bourbon" (Bourbon is an old name for the island of La Réunion). This explains the wrong locality information "Réunion", which was later corrected to "Nossi-Be et Nossi-Cumba" in one MNHN catalogue, and to "Madagascar" in a second catalogue. We consider also the Nosy Be - Nosy Komba locality information as wrong (see below).

Material examined - BMNH 1947 2 7.19 (holotype, Madagascar, leg. R. BARON), BMNH 95 7 4 34-6, BMNH 96 12 2 28-31 (Ambohitombo forest, coll. FORSYTH MAJOR [1 specimen exch. Vienna 1912], NIL), BMNH 1925 7 13 1-6 (Madagascar, coll. FORSYTH MAJOR, NIL), BMNH 1925 7 2 57 (Antsihanaka, purch. ROSENBERG), BMNH 1930.2.2.1 (Analamazoatra forest, environs of Périnet, purch. ROSENBERG), BMNH 1953 1 5 42-5 (Madagascar, pres. G. W. ALLAN); MNHN 6807, MNHN 1991 2846-7 (ex MNHN 6807, "Nosy Komba", paralectotypes of *Phrynomantis maculatus*), MNHN 1991.2845 (ex MNHN 6807A; lectotype of *Phrynomantis maculatus*, "Nosy Komba"); MNHN 1883.584 (locality unknown, ded. HUMBLLOT), MNHN 1902 335 (Ikongo; M. Besch), MNHN 1907.161-2, MNHN 1991 1813 (locality unknown, obtained from the "section de Madagascar à l'Exposition coloniale de Marseille", ex MNHN 1907 162, 162A); MNHN 1931 14 (locality unknown), MNHN 1991.1807-9 (locality unknown, ex MNHN 1931 14 A-C), MNHN 1931.15 (Moramanga), MNHN 1991 1810-2 (Moramanga, ex MNHN 1931.15 A-C), MNHN 1931.16-7 (SE Fianarantsoa, DLcary 1926-1930), MNHN 1933 247 (Ruisseau d'Iorantjatsy, Distr. Fianarantsoa, alt. 1000 m), MNHN 1936 40-2 (Forêt de Tsianovoha); MNHN 1936 43-6 (probably "forêt de Tsianovoha", HLM), MNHN 1953 135 (Anosibe [Moramanga]), MNHN 1972 775-6 (Moramanga), MNHN 1976 233-4 (locality unknown); MNHN 1988 7599 (locality unknown, don. O. BEHRA III 1988), MNHN 1993 1441-2, MNHN 1993 1444, MNHN 1993.1446-7 (locality unknown), ZFMK 14208 (Niagarakely, leg. H. MEIER 1972), ZFMK 28870-2 (Ambohitombo forest; leg. FORSYTH-MAJOR 1903, originally Museum Gottingen), ZFMK 46035-8 (locality unknown, through pet trade, 46035 CS), ZFMK 47008-9 (Moramanga, leg. R. SEIPP IV 1987), ZFMK 48054-60 (120 km S Moramanga Marolamba, leg. H. MEIER III 1988, 48055 CS), ZFMK 50161 3 (Moramanga, leg. H. MEIER II 1989), ZFMK 50551 (Moramanga, leg. F. W. HENKEL, W. SCHMIDT & V. MILLER 1989), ZFMK 56165-9 (through pet trade, ded. F. GLAW XI 1993), ZFMK 62242 (Mantady, leg. F. GLAW II 1996), ZFMK 62718-21 (locality unknown, CS), ZFMK 62722 5 (locality unknown, TE), ZFMK 62287-8 (juveniles) and 64139-40 (all Volohparara, leg. F. GLAW, D. RAKOTOMALALA & F. RANAIVOAJONA III 1996, TE), MRSN A0061 1-4 (Andasibe, Amalonahe, leg. F. ANDRIONE 2 XII 1991), MRSN A0066 1-5 (Vatoharanana-Ranomafana, c/o Ifanadiana, leg. F. ANDRIONE 8 II 1993, NIL), MRSN A0067 1 5 (Volohparara, leg. F. ANDRIONE 9 II 1993), TM 9890, 9896, 9900 (Analamazoatra, leg. METHUEN).

The following somewhat deviating specimens are also attributed to *M. baroni* in a preliminary way (see discussion below): TM 9888 9, 9892, 9895, 9896-9 (Folohy, coll. MITHRAN), TM 9894 (Folohy, coll. HIRSCHELL-CHAUVIN), BMNH 1986 2 (Camp 4, Zahamena, 17° 40' S, 48° 50' W, leg. C. J. RAXWORTHY 8 IX 1985).

Distribution. The species of the *M. cowani* and *M. madagascariensis* groups (as defined in the present study) were insufficiently distinguished in previous works. The corresponding distribution maps (mainly in BLOMMERS-SCHLOSSER & BLANC, 1991, as *M. madagascariensis* and *M. cowani*) did not contain references to literature records or voucher specimens. GLAW & VENCES (1994) assigned some localities to the species *haraldmeieri*, *cowani*, *pulchra* and "loppei", but most localities remained without reliable attribution to any species.

The distribution map of BLOMMERS-SCHLOSSER & BLANC (1991) was mainly based on MNHN voucher specimens. All of these were examined by us. This allows us for the first time to outline the distribution of the different species with a certain reliability. *M. baroni* occurs in the central Eastern Region, mainly at mid-altitude localities: [1] Antsihanaka; [2*] Ankeniheny (ca 1000 m altitude), [3*] An'Ala (ANDREONE, 1993, DALY et al., 1996; personal observation at ca 840 m altitude); [4*] Analamazoatra; [5] Anosibe (Anosibeana), [6] Niagarakely, [7] Marolamba (120 km S Moramanga; probably identical with Marolambo, which is situated about 100 km S Moramanga, see BLOMMERS-SCHLOSSER & BLANC, 1993); [8] Ambohimombo, [9] Ikongo; [10] Ruisseau d'Iorantjatsy; [11] Forêt de Tsianovoha, [12*] Ranomafana National Park (ANDREONE, 1992; GARRAFFO et al., 1993; personal observation near Vohiparara, ca. 1000 m altitude), [13*] Mantady. Additional localities were published by DALY et al. (1996). [14] Sahavondrona (near Ranomafana; ca 1000 m altitude), [15] 30-35 km south of Moramanga.

Two additional localities, [17] Folohy and [18] Zahamena (TM and BMNH vouchers, see above) are attributed to *M. baroni* only in a preliminary way. These specimens, which unfortunately have largely faded color patterns, show a deviating coloration which resembles *M. nigricans* in many respects. In the Folohy sample, the ventral side including the femur is dark with small (not large as usually in *M. baroni*) rounded light spots (no horseshoe marking). The tibia and the foot are light (except TM 9888 which has a dark tibia). The flank blotches are large and rounded, as typical for *M. baroni*. The rostral stripe appears indistinct without sharp borders, and the head surface may have been lighter than the back in life. The single known Zahamena specimen, according to the attached field label, had the following life coloration "Back and legs vivid bright green, flanks black, lower back and legs brown, belly black with pale blue spots, iris black". In preservative, the pattern is largely faded. Femur and tibia are dark, but the foot is light ventrally and dorsally. The existing information on these specimen does not allow for further statements, in the distribution map, we list the two localities as intermediate between *M. baroni* and *M. nigricans*. The color and pattern information given below for *M. baroni* applies to all populations except for Folohy and Zahamena.

The remaining localities listed by BLOMMERS-SCHLOSSER & BLANC (1991) for *M. madagascariensis* can be assigned as follows. Marojejy refers to *M. nigricans*, Antsihanaka is the type locality of *M. pulchra*, Marolambo is the type locality of *M. loppet* (junior synonym of *M. madagascariensis* according to the present study), and seems also to be a locality of *M. baroni* (see above, if Marolambo and Marolamba are identical), Ambalavato is the type locality of *M. madagascariensis*; Iremo, Ambatodradama and Betafo refer to *M. cowani*, Chaînes Anosyennes, Ambana, Bekazaha and Soavala refer to *M. haraldmeieri*; Ivohibe and Marovitsika refer to *M. aff. baroni* which is here considered separately (see below).

We propose to delete the localities Nosy Be and Nosy Komba (which are based on a dubious locality information referring to the types of *Phrynomantis maculatus*, see above). As discussed by GLAW & VENCES (1994), these localities are in the Sambirano region where recent extensive surveys have only yielded records of species of the *M. betsileo* group. We also propose to ignore the locality Ambohidratrimo, located 20 km NW of the Malagasy capital Antananarivo (VIETTE, 1991) near the Ivato airport. No vouchers for this locality were found in the MNHN. The presence of habitat structures suited for species of the *M. baroni* group or *M. madagascariensis* group is not probable at this locality for the last 100 years.

Diagnosis. – (1) *Morphology*: A large, slender *Mantella*. SVL 22–30 mm. TTA mostly reaching the eye center but at least the tympanum. Terminal disks of fingers and toes expanded. Tympanum/eye ratio generally 3/5. IMT small (ratio width/length about 4/5). – (2) *Dorsal color and pattern*: Head, dorsum and flanks deep black, without dorsolateral color border. Frenal stripe absent. Yellowish rostral stripe present, generally not in contact with flank blotch. Forelimb (except the mostly black fingers) and femur yellow to greenish. This color continuing onto the flanks, forming relatively large, rounded flank blotches. These sometimes dorsally expanding onto the back, not being delimited by the dorsolateral border. Size of blotches variable, but in none of the examined specimens blotches of opposite flanks contacting each other on the back. Tibia, tarsus and foot orange with irregular black crossbands and markings. No flashmarks. Iris completely black without light pigment. (3) *Ventral color and pattern*: Venter, throat and limbs black with few relatively large, rounded light markings which are generally not blueish but yellow to greenish. No horseshoe marking, throat with only a single rounded marking, sometimes completely black. Tibia, tarsus and foot orange as dorsally, but mostly without black patterns. The orange color sometimes reaching the distal part of the femur but not further proximally. Exceptionally, single specimens with a nearly complete horseshoe marking (observed in one specimen of the series MRSN A0066).

***Mantella* aff. *baroni* (from Andringitra)**

Chresonyms

Mantella covarr GUIBÉ, 1964 (part.: fig. 4-6), 1978 (part.)

Mantella madagascariensis BLOMMERS-SCHLÖSSER & BLANC, 1991 (part.), 1993 (pl. 19 fig. 104); GLAW & VENCES, 1994 (part.)

Mantella madagascariensis sensu stricto GLAW & VENCES, 1992a (part., see localities and fig. 180)

Mantella madagascariensis madagascariensis BUSSE, 1981 (part.: fig. 5)

Identity: Within and between the known populations of *Mantella baroni*, the dorsal and ventral coloration of adults as described above is rather uniform (see also ANDRIONGE, 1992; GLAW & VENCES, 1994). On the contrary, specimens from Andringitra (south of all other known localities of *M. baroni*) differed by an enormously variable dorsal pattern (see below). We here consider the Andringitra population as a separate form *Mantella* aff. *baroni* which clearly is very closely related to *M. baroni*. Final clarification of its status is not possible at present.

Comment. – No scientific name is currently dispicable for this form

Material examined – The following specimens can clearly be assigned to this form due to their largely extended dorsal green-yellow pattern MNHN 1953 136 (Col d'Ivohibe, Andringitra), MNHN 1991 1800-4 (Col d'Ivohibe, Andringitra; ex MNHN 1953 136 A-E); MNHN 1972.767, MNHN 1972 769-72, MNHN 1972 774, MNHN 1972 777-8 (Col d'Ivohibe, forêt Marovitsika).

Several other specimens differ from typical *M. baroni* only by a gradually larger extension of the yellow pattern. These are MNHN 1991 1805-6 (Col d'Ivohibe, Andringitra; ex MNHN 1953 136 G-H); MNHN 1972 763-6 (Col Ivohibe, forêt Marovitsika), MNHN 1972 768, MNHN 1972 773 (Col Ivohibe, forêt Marovitsika) MNHN 1991 1805 is most similar to typical *M. baroni* by dorsal pattern MNHN 1972 763-5 are very large and stout specimens, probably females.

Distribution – Only known from the Col d'Ivohibe [1] in the Andringitra massif.

Diagnosis. (1) *Morphology*: A large, slender *Mantella*. SVL 27-31 mm, females 30 mm. TTA reaching eye center in some specimens, but only to forelimb insertion or slightly beyond in large females. Terminal disks of fingers and toes expanded. Tympanum/eye ratio generally 1/2 to 3/5. IMT small. (2) *Dorsal color and pattern*: In some specimens similar to typical *M. baroni*, but with a larger extension of the yellow flank blotches which reach widely onto the dorsum (coloration observed in all specimens identified as females) Other specimens, by general body proportions possibly mainly males, showing a broad dorsal contact of the flank blotches, or a further increase of these, resulting in a nearly uniformly yellow pattern dorsally (see GUIBÉ, 1964, fig. 4-6, BUSSE, 1981: fig 5), with the yellow color also extending onto the tibia, which is otherwise orange with black. No flashmarks. Iris seemingly with some light pigment in its upper part according to the color plate in BLOMMERS-SCHLÖSSER & BLANC (1993, here reproduced in black-and-white on fig. 2) which shows a specimen relatively similar to typical *M. baroni*, with a (very indistinct) dorsolateral color border. Rostral stripe present and generally in contact with the flank blotches. In specimens with large extension of yellow color, the rostral stripe is the sharp border between yellow dorsal and black lateral color of the head. (3) *Ventral color and pattern*: Similar to *M. baroni*, but with a higher number and smaller size of light markings (intermediate between *M. baroni* and *M. haraldmeieri*). Information on the color of the light markings in life not available.

Mantella cowani Boulenger, 1882

Mantella cowani Boulenger, 1882. *Name-bearing type* lectotype, by present designation, BMNH 1947 2 7 4 (ex BMNH 82 3 16 38), female according to BOULENGER (1882), SVL 28 2 mm. *Type locality* "East Betsileo", according to the original description and the BMNH catalogue. *Other types* paralectotype, following present lectotype designation, BMNH 1947 2 7 5 (ex BMNH 82 3 16 39), female according to BOULENGER (1882). *Etymology* named after the collector of the type series, Reverend W. DEANS COWAN.

Mantella cowani DALY et al., 1996; STANISZEWSKI, 1998a (fig.)

Mantella Cowani MOCQUARD, 1909

Mantella cowani WERNER, 1901, MATHÉLÉN & HEWITT, 1913, PARKER, 1925, GIBBÉ, 1964, 1978 (part.)

BUSSE, 1981 (syn. *madagascariensis*), BLOMMERS-SCHLÖSSER & BLANC, 1991 (part.), BÖHME et al.,

1993; VENCES et al., 1994, GLAW & VENCES, 1994, BARTLETT, 1995 (fig. p. 24); CARISSIMI PRIORI,

1995 (fig. p. 43); STANISZEWSKI, 1997a (fig.), 1997b (fig.); LARSEN, 1997; VENCES & KNILL, 1998

Mantella cowani s. str.; ANDREONE, 1992 (p. 438).

Other chresonyms

Mantella madagascariensis: BLOMMERS-SCHLÖSSER & BLANC, 1991 (part.)

Mantella madagascariensis madagascariensis: BUSSE, 1981 (part.)

Mantella madagascariensis nigricans: BUSSE, 1981 (part.), MNHN 9594 on p. 33)

Mantella madagascariensis (color morph *Mantella "cowani"*): GLAW & VENCES, 1992a

Identity. – See BÖHME et al. (1993) and VENCES et al. (1994) for the confusing taxonomic history of the taxon. The species is well distinguished by its typical pattern.

Comments. (1) Lectotype and paralectotype are in excellent state of preservation. The typical pattern is still recognizable, although the red color has largely faded. (2) Although the specific name was written *cowanii* in the original description, we here continue using the spelling *cowani* which was used by most subsequent authors, since the *Code* allows both spellings to be used.

Material examined. BMNH 1947.2.7.4-5 (lectotype and paralectotype, E-Betsileo; leg. W. D. COWAN); MNHN 1906.171, MNHN 1991.2844 (Betafo), MNHN 1973.528-9 (Ambatomenaloha, massif Itremo); MNHN 9594 (Ambatodradama, 2000 m, ARNOULT 11 XII.1962), ZFMK 59822 (locality unknown, ded. F. GLAW IV.1995), ZFMK 62726-7, ZFMK 62729-31 (locality unknown, TE), ZMB 10404, ZMB 50106-7 (East-Betsileo; leg. HILDEBRANDT).

Also the following specimens with unknown locality are considered as *M. cowani* based on unpublished electrophoretic and morphometric data: ZFMK 62728 (TE, color in life yellow/black instead of red/black); ZFMK 62719, ZFMK 62721 (TE, color in life yellow/black instead of red/black, and extension of yellow color intermediate between *M. cowani* and *M. baroni*).

Distribution. The type locality "East Betsileo" comprises a large area and does not represent a concrete locality. According to a personal communication of A. PEYRIERAS, the species occurs: [1] in forested regions of the highlands SE of Ambatolampy and [2] near Antoetra. MNHN vouchers corroborate the localities [3] Betafo, [4] Itremo and [5] Ambatodradama. See the discussion in the section on distribution of *M. baroni*.

Diagnosis. (1) *Morphology.* A large, slender *Mantella*, SVL 22-29 mm, TTA mostly not reaching the eye but between forelimb insertion and tympanum (only reaching forelimb insertion in a few specimens). Terminal disks of fingers and toes nearly not expanded. Tympanum/eye ratio generally 1/2-3/5. IMT medium-sized (ratio width/length about 2/3). (2) *Dorsal color and pattern.* Head, dorsum and flanks deep black. Rostral and frenal stripes absent. Proximal part of femur and humerus generally red (exceptionally orange or yellow). This color extending on the flanks as small flank blotches, and also present as a broad band on tarsus and foot (sometimes disrupted by black markings). A light spot below the eye sometimes present. All remaining dorsal surface uniformly black. No flashmarks. Iris completely black without light pigment. (3) *Ventral color and pattern.* Black with relatively large, circular whitish-blue markings. Single markings on throat, but no horseshoe marking. Limbs also black with whitish-blue markings, except broad red bands on tibia, tarsus and foot which correspond to those on the dorsal surface.

Mantella haraldmeieri Busse, 1981

Mantella madagascariensis haraldmeieri BUSSE, 1981. *Name-bearing type* holotype by original designation (BUSSE 1981:34), ZFMK 25351 male, SVL 22.0 mm. *Type locality* Fort Dauphin, Sud-Madagascar" according to original description and ZFMK catalogue. – *Other types*, paratypes, ZIMK 21805-7, ZFMK 25352. *Etymology*, named after the German amateur herpetologist Harald MEIER who collected the types. *Mantella madagascariensis haraldmeieri*, BOHME & BISHOPP, 1984, MLR, 1986. *Mantella haraldmeieri*, PINTAK, 1990; ANDRIANON, 1992 (plate IV, fig. 5-6); GLAW & VENCES, 1992a, 1992b (fig. p. 28); ANDRIANON, 1993 (fig. 2); BOHME et al., 1993; HERRMANN, 1993 (fig.); VENCES et al., 1994 (fig. p. 392); GLAW & VENCES, 1994; HENKEL & SCHMIDT, 1995 (fig. p. 53); STANIS/WSKI, 1997b (fig.); LARSEN, 1997; PINTAK et al., 1998; VENCES et al., 1998; VENCES & KNILL, 1998.

Other chresonyms.

Mantella Cowani. MOCQUARD, 1902.

Mantella cowani BACHMANN & BLOMMERS-SCHLÖSSER, 1975, BLOMMERS-SCHLÖSSER, 1978, 1979a; BLOMMERS-SCHLÖSSER & BLANC, 1991 (part.), 1993 (pl 19 fig. 103)

Mantella betsileo MEIER, 1980 (part., p. 353, second fig. above), BUSSE, 1981 (part. tab. 1, specimens from Anosyennes).

Identity. – *M. haraldmeieri* has been generally considered as a separate species in recent years (see BÖHME et al., 1993), mainly based on color patterns as (1) a light dorsum sharply bordering the dark flanks, (2) dorsally uniform hindlimb coloration and (3) small, beige flank blotches. MNHN specimens from the Anosy mountains (Chaînes Anosyennes) in southern Madagascar, near the *haraldmeieri* type locality Tolagnaro, were erroneously identified as *Mantella betsileo* by BUSSE (1981). A detailed re-examination of this large series showed that all specimens are clearly to be assigned to *M. haraldmeieri* based on color patterns (1)-(3) as defined above, and further on (4) presence of an unforked sternum (VENCES et al., 1999a), (5) lack of a horseshoe marking, (6) presence of small, rounded light spots on the venter, and (7) ventrally uniformly light colored tibia, tarsus and foot

In most MNHN specimens, the dorsolateral coloration border is very indistinct or absent; we presume that the dorsal darkening was caused by the formalin fixation to which the specimens most probably have been exposed (see section on *M. nigricans*). In fact, in at least one specimen (MNHN 1973.511), the coloration border is still clearly recognizable.

In several MNHN specimens, the flank blotches are larger than described until present for *M. haraldmeieri* (see fig. 10), indicating the close relationships of *M. haraldmeieri* with the remaining species of the *M. cowani* group.

Comments (1) *M. haraldmeieri*, according to our personal observations, does not occur in the coastal town Fort Dauphin (Tolagnaro), the type locality, itself, but in nearby rainforest remains near Nahampoana (2) Probably due to a typing error, BUSSE (1981) did not mention the specimen ZFMK 25353 which has similar collection data as the holotype and paratypes, and was listed in the appendix of BUSSE's (1981) work. Although this specimen was originally catalogued as paratype, it cannot therefore be considered as such (and was not listed in the account of BÖHME & BISCHOFF, 1984).

Material examined MNHN 1901 232 (Fort Dauphin, envoi de M. ALLUAUD, pigments totally faded, identification by size, locality and medium-sized IMT); MNHN 1973 499 (Soavala-Ambana, Chaînes Anosyennes), MNHN 1973 500 (Beampigaratra, Nord Bekazaha, alt. 950 m), MNHN 1973 501 (Camp IV^o), MNHN 1973 502-11 (Camp IV, Ambana), MNHN 1973.512-16 (Camps IV et III bis), MNHN 1973 518-20 (Camps IV et III bis), MNHN 1973 521 7 (Ambana), ZFMK 21805-7 (Fort Dauphin, leg. H. MEIER 1978, paratypes), ZFMK 25351 (Fort Dauphin, leg. H. MEIER 1978, holotype), ZFMK 25352 (Fort Dauphin, leg. H. MEIER 1978, paratype), ZFMK 25353 (Fort Dauphin, leg. H. MEIER 1978), ZFMK 47831-3 (Fort Dauphin, leg. H. MEIER 1988), ZFMK 48181-2 (Fort Dauphin, leg. F. W. HENKEL & R. SEIPP 1988), ZFMK 52741-3 (Nahampoana near Fort Dauphin, leg. F. GLAW & M. VENCES 1991, 52741 CS), MRSN A0062 1-2 (Nahampoana, leg. F. ANDREONT 14 IV 1990), MRSN A0063 (Nahampoana, leg. R. NINCHERI 14 IV 1990).

Distribution – ZFMK specimens with a reliably known locality were collected in [1*] near Nahampoana. A. PIYRIJAS (personal communication) found the species in [2] Mahatalaha. MNHN vouchers demonstrate that the species is the only *Mantella* so far known in the Anosy mountain chain. Localities are [3] Chaînes Anosyennes; [4] Ambana; [5] Bekazaha; [6] Soavala. See the discussion in the section on distribution of *M. baroni*

Diagnosis. (1) *Morphology.* A medium sized to large, relatively slender *Mantella*. SVL 21-27 mm. TTA mostly reaching the eye center but in some specimens only the tympanum. Terminal disks of fingers and toes expanded. Tympanum/eye ratio generally 3/5. IMΓ medium-sized (ratio width/length about 2/3). (2) *Dorsal color and pattern:* Dorsum light brown with three regular dark brown patterns: (a) an either triangular or inversely Y-shaped marking in the shoulder region; (b) a larger, heart-shaped marking at the center of the dorsum; and (c) two spots in the anal region. Flanks dark brown, with a sharp dorsolateral color border. Hindlimbs yellowish-brown with indistinct darker crossbands. Forelimbs cream to beige. Color of limbs extending as mostly rather small flank blotches on the flanks. No flashmarks, postero-dorsal part of femur and knee hollow orange, but without contrast to the surrounding surface. Upper part of iris light. – (3) *Ventral color and pattern:* Forelimb, femur, venter and throat black with many small rounded whitish blue spots. On the throat, these whitish blue spots sometimes are arranged semicircularly along the lip, but they are not fused (not forming a closed horseshoe marking). Foot, tarsus and tibia orange-red. This color sometimes extending onto the distal part of the femur.

***Mantella nigricans* Guibé, 1978**

Mantella *cowani nigricans* Guibé, 1978. *Name-bearing type* lectotype, by present designation, MNHN 1973 555, female, SVL 26.3 mm. *Type locality* "massif du Marojezy", according to original description. *Other types* paralectotypes, following present lectotype designation, MNHN 1973 517, MNHN 1973 530-54, and MNHN 1973 556-9. *Etymology* derived from Latin *nigrare* (to darken towards black), referring to the uniformly dark color of the type series which, however, was most probably caused by fixation in formalin.

Mantella madagascariensis nigricans BUSSE, 1981 (part, not MNHN 9594), BLOMMERS-SCHLÖSSER & BLANC, 1991; GLAW & VENCES, 1994 (nomen dubium; p. 412)

Mantella nigricans; VENCES & KNIEL, 1998; STANISZEWSKI, 1998a

Mantella "negrinata" [conditional name]; LARSEN, 1997

Mantella new species. STANISZEWSKI, 1997a (fig. p. 11 and 16)

Mantella sp. VENCES et al., 1998

Other chresonyms

Mantella madagascariensis; GLAW & VENCES, 1994 (part.).

Mantella madagascariensis sensu stricto GLAW & VENCES, 1992a (part.; locality Marojezy)

Identity. – The name was erected by GUIBÉ (1978: 84) as the subspecies *Mantella cowani nigricans*. No types were designated. The original description was very short and superficial: "Parfois, au contraire, les taches claires de la racine des membres se réduisent considérablement et finissent par disparaître, le corps et les pattes sont alors uniformément noirs. De tels individus mélangés se rencontrent en particulier dans le massif du Marojezy, ils correspondent à une sous-espèce. *M. cowani nigricans* n. subsp."

BUSSE (1981) and BLOMMERS-SCHLÖSSER & BLANC (1991: 274) accepted the subspecies in a preliminary way. BUSSE (1981), however, doubted the locality Marojezy and assigned MNHN vouchers from Betafo and Ambatodradama to *nigricans* (these specimens, however, belong to *M. cowani*, see above).

During examination of *Mantella* voucher specimens in the MNHN we noted that all specimens from Marojezy are identified as *Mantella cowani nigricans* in the catalogue. The whole series was catalogued in 1973, while the batrachological MNHN collection was curated

by Jean GUIBÉ. In all these specimens, the light color pattern is largely faded, very probably due to a previous formalin fixation, giving the impression of melanistic specimens. There is little doubt that GUIBÉ's description was based on these specimens, which must therefore be considered as syntypes.

Unfortunately, the syntype series is not homogeneous, it contains some specimens of *M. laevigata* as well as a rather large sample of specimens of a *M. cowani* group species which differs from all other members of the group (see below). In order to reach stability of the name, we here designate one of these specimens as lectotype. This avoids the necessity of creating a new name for the Marojejy populations belonging to the *M. cowani* group.

Mantella nigricans belongs to the *M. cowani* group based on: (1) single click calls (GLAW, personal observation); (2) unforked sternum (VENCES et al., 1999a); (3) lack of horseshoe marking; (4) rounded and isolated ventral spots, (5) lack of a frenal stripe; (6) presence of flank blotches. It differs from all other members of the group by lacking red ventral color on the hindlimbs. Furthermore, it differs from *M. cowani* and *M. baroni* by smaller ventral spots and a different dorsal extension of light (green) color, and from *M. haraldmeieri* by a different dorsal coloration. *M. nigricans* is most similar by dorsal coloration to some specimens of *M. aff. baroni*.

Comment – Of the paralectotypes, only the specimens listed in the *Material examined* section are conspecific with the lectotype; see section of *M. laevigata* for the remaining specimens.

Description of lectotype - MNHN 1973 555, female specimen with nearly mature oocytes. Specimen in good state of preservation with a longitudinal central cut along the venter. Stomach and intestine removed for content analysis and stored separately in small tubes. For measurements, see tab. 2. Body slender, head not broader than body; snout slightly pointed in dorsal, rounded in lateral view; nostrils directed laterally, not protuberant, nearer to tip of snout than to eye, canthus rostralis weak, straight; loreal region even; tympanum rather indistinct, medium-sized, rounded, its diameter about half of eye diameter; supratympanic fold weakly developed; tongue longish to ovoid, slightly bifid posteriorly, maxillary and vomerine teeth absent, choanae small, rounded. Arms slender, subarticular tubercles single, outer metacarpal tubercle rounded, inner metacarpal tubercle rounded, both rather distinct and of similar size; fingers without webbing; finger length $1 < 2 < 4 < 3$, finger 4 distinctly longer than 2; finger 2 only slightly longer than 1, faintly developed but distinct terminal finger disks. Legs moderately robust, tibiotarsal articulation reaching posterior eye margin, feet with small, slightly elliptical inner and rounded outer metatarsal tubercles; subarticular tubercles single, rounded; toe disks faintly developed but distinct. Foot without webbing. Lateral metatarsalia connected; toe length $1 < 2 < 3 < 5 < 4$, toe 3 distinctly longer than 5. Skin on the upper surface smooth, ventral surface smooth, except for granular thigh patches ("femoral glands") extending from the anus ca. 6 mm distally (max width 3.6 mm). Color in life unknown, in preservative almost uniformly dark brown, with very little pattern contrast (probably due to formalin fixation). Contours of moderately large light flank blotches faintly recognizable. Venter and ventral side of fore- and hindlimbs, including humerus, fibula, femur, tibia, tarsus and foot, uniformly dark with small rounded light spots. Six spots positioned on the throat along the lip, but not fused to form a horseshoe-marking. No spots in the breast area. No flashmarks.

Material examined MNHN 1973.555 (Marojezy, 600 m, lectotype), MNHN 1973.541 (Marojezy, 300 m, paralectotype), MNHN 1973.530-3, MNHN 1973.550-4, MNHN 1973.556, MNHN 1973.559 (Marojezy, 600 m; paralectotypes); ZFMK 59887-8, ZFMK 59902 (Marojezy Camp 3; leg. F. GLAW & O. RAMILISON II 1995); MRSN A1822 (Tsararano Chaim, Camp 2, leg. F. ANDREONE 10.XII 1996), MRSN A1823 1-4, MRSN A1824 1-2, MRSN A1825 (Tsararano Chaim, Camp 1; leg. F. ANDREONE XI-XII 1996), MRSN A1829.1-8 (Analabe/Anjanaharibe, Camp 2; leg. F. ANDREONE II 1996), MRSN A1830 (Analabe/Anjanaharibe, near Camp 2 at about 1200 m, leg. F. ANDREONE II 1996)

Distribution. Known from: [1*] the Marojezy massif (North-Eastern region, 300-700 m altitude); [2] Hiaraka (Iaraka) (Masoala peninsula; A. PEYRIERAS, personal communication), [3] Tsararano (700 m altitude), [4] Anjanaharibe (1200 m altitude). See the discussion in the section on distribution of *M. baroni*.

Diagnosis (1) *Morphology*: A medium sized to large, relatively stout *Mantella*. SVL 27-28 mm. TTA reaching the forelimb insertion or the tympanum. Terminal disks of fingers and toes rather largely expanded. Tympanum/eye ratio generally slightly below 3/5. IMT medium-sized (ratio width/length 2/3 to 4/5). - (2) *Dorsal color and pattern*: Relatively variable. Some specimens similar to *M. pulchra* (see below). Flanks black, with a sharp dorsolateral color border. Limbs brown, except humerus and proximal femur; these light green to yellowish green, this color extending as relatively large flank blotches onto the flanks. In other specimens the green color making up the major part of the dorsal surface, including dorsum and flanks (in one specimen the anterior two thirds of the dorsal surface were green) In these cases, however, a strong dorsolateral color border remains on the head. No sharply delimited rostral stripes and no flashmarks. Iris with light pigment in its upper part. (3) *Ventral color and pattern* Black with small, rounded blue spots. On the throat these spots sometimes arranged semicircularly along the lip, but only exceptionally fusing to form a closed horseshoe marking

Mantella bernhardi group

Mantella bernhardi Vences, Glaw, Peyrieras, Bohme & Busse, 1994

Mantella bernhardi Vences, Glaw, Peyrieras, Böhme & Busse, 1994. *Name-bearing type* holotype by original designation (VENCES et al., 1994: 391), ZFMK 57164, male, SVL 39.0 mm. *Type locality* "Regenwald nahe Tolongoïna, Provinz Fianarantsoa", according to the original description. *Other types*: none. - *Etymology*: named after the German zoologist Bernhard MÜLLER

Mantella bernhardi: GLAW & VENCES, 1994, CARISSIMI PRIORI, 1995 (fig. p. 43), STANISZEWSKI, 1996 (plate p. 26), 1997a (fig. 1), 1997b (fig. p. 21, 40-41, 60 above and middle, probably not fig. p. 37 and 60 below), 1998a (fig.), VENCES et al., 1998

Material examined ZFMK 57164 (S-Mad E-Betsileo [forest near Tolongoïna *vide* PEYRIERAS], ded M VENCES, III 1994, leg. A. PEYRIERAS, holotype), ZFMK 59820-1 (near Tolongoïna, leg. PEYRIERAS, ded F. GLAW IV 1995), ZFMK 62697-8 (locality unknown, CS), ZFMK 62699-707 (locality unknown, TE) MRSN A1964 (Ambohimana next to Tolongoïna, leg. F. ANDREONE 20 VII 1995)

Distribution Until now, the species is only known from the type locality: [1] forest near Tolongoïna This locality is corroborated by the observation of F. ANDREONE (personal communication) who, however, found only one single specimen in the dry season

Table 2 Morphometric measurements of *Mantella* type specimens, and of a reference specimen of *M. milotoypanum* (ZFMK 65626). Stat, Status; HT, holotype, PT, paratype, LT, lectotype, PLT, paralectotype, TOT, topotype, M, male, F, female, TT, point that is reached by the tibiotarsal articulation when limbs are adpressed along the body. 1, forelimb insertion; 2, nearly to tympanum, 3, tympanum, 4, between tympanum and eye; 5, posterior eye margin, 6, center of eye. See *Materials and methods* section for abbreviations of measurements. Most specimens could not be reliably sexed, generally due to bad state of preservation. Measurements of inner metatarsal tubercle and disk width on third finger were only taken from few equally well fixed specimens. Other lacking measurements are due to damage or bad preservation of the respective specimens.

Collection number	Sex	Stat	SVL	HW	HL	Eye	Tym	Eye-Ns	Ns-St	ForL	Hal	HtL	FoTL	FoL	ToLI	DW3	FW3	IMTL	IMTB	IMTH	TT
<i>Mantella betsileo</i>																					
MNH 1895 278		LT	190	61	82	27	14	19	14	132	6.0	29.1	13.8	8.7	11	0.37	0.32	0.79			6
MNH 1895 279		PLT	157							10.4		25.3									6
<i>Mantella atemsi</i> (syn. <i>Mantella betsileo</i>)																					
NMW 20837	F	LT	256	72	92	26	15	21	13	163	7.1	34.7	16.5	11.4	17	0.7	0.4	0.8	0.4	0.3	5
ZMB 16588	M?	PLT	217	64	94	24	17	20	11	146	6.4	33.6	14.8	9.7							6
<i>Mantella viridis</i>																					
ZFMK 47900	F	HT	303	89	114	28	20	23	20	177	8.0	39.5	18.8	12.8	17	0.95	0.68	1.05	0.75		1
<i>Mantella expectata</i>																					
ZFMK 53540	M	HT	234	77	95	29	15	20	15	158	6.7	34.8	17.1	11.4	11	0.78	0.43	0.85	0.50	0.30	5
ZFMK 53541	F	PT	220	68	86	24	14	18	14	144	6.3	34.8	16.0	10.9	15	0.73	0.45	0.75	0.53	0.35	6
ZFMK 53542	M	PT	220	68	86	24	14	18	14	144	6.3	34.8	16.0	10.9	15						6
ZFMK 59095		PT	249	76	100	26	16	16	16	155	7.4	36.6	17.0	11.4	14	0.70	0.60	0.85	0.58	0.23	6
ZFMK 59096		PT	213	81	98	28	17	20	15	152	7.0	35.1	16.6	11.1	11	0.73	0.58	0.90	0.63	0.30	5
ZFMK 59097		PT	214	75	94	27	16	17	16	166	6.4	33.8	16.4	10.7	12						6
ZFMK 59098		PT	236	72	89	28	16	17	12	154	7.4	34.5	16.6	10.8	14						6
<i>Mantella laevigata</i>																					
TM 10074		HT	225	69	90	24	12	17	16	149	6.8	33.2	15.3	9.6	18	1.1	0.4	0.7	0.3	0.3	6
TM 10085		PT	253	73	92	25	12	16	14	173	8.2	38.2	17.6	10.4	18	1.1	0.4	1.0	0.4	0.4	5
TM 10086		PT	245	78	103	26	13	22	17	163	7.4	36.3	16.4	10.5	19	1.2	0.4	0.9	0.4	0.4	5
TM 10087		PT	244	68	100	26	13	17	19	160	7.8	36.8	16.3	10.0	20	0.8	0.3	1.0	0.4	0.5	6
TM 10088		PT	204	62	86	24	11	17	11	140	5.7	31.6	13.9	8.9							6
TM 10090		PT	174	53	78	20	09	15	10	115	4.6	26.4	10.8	6.9							5
<i>Mantella haroni</i>																					
BMNH 1947 27 19	M	HT	272	73	109	28	16	22	17	161	7.1	36.1	17.2	11.1	16						3

Collection number	Sex	Stat	SVL	HW	HL	Eye	Tym	Eye-Ns	Ns-St	ForL	HaL	HiL	FeTL	FoL	ToL1	DW3	FW3	IMTL	IMTB	IMTH	IT
<i>Phrynomantis maculatus</i> (syn. <i>Mantella baroni</i>)																					
MNHN 1991 2845		LT	27.0	7.5	10.9	2.9	1.5	2.0	1.6	17.7	7.7	40.4	18.6	12.4	1.7	0.69	0.46	0.83		0.30	3
MNHN 1991 2846		PLT	26.2	7.6	10.1	3.2	1.5	2.1	1.6	16.9	7.0	39.4	17.2	11.0	1.9	0.57	0.43	0.86		0.44	5
MNHN 1991 2847		PLT	24.9	8.1	9.0	3.1	1.3	2.1	1.6	16.9	7.5	38.4	18.3	11.7	1.6						5
MNHN 6807	F	PLT	28.4	8.0	10.2	2.9	1.9	2.2	1.8	17.2	7.3	39.1	17.5	11.2	1.4	0.61	0.38	1.16		0.51	3
<i>Mantella cowani</i>																					
BMNH 1947 2 7 4		LT	28.2	7.5	10.1	2.8	1.3	1.9	1.6	16.5	7.3	35.8	17.4	11.5	1.6	0.6	0.5	1.0	0.4	0.4	1.2
BMNH 1947 2 7 5		PLT	27.5	7.5	10.3	2.7	1.4	2.0	1.6	16.7	7.1	37.4	18.2	12.3	1.8	0.7	0.6	1.1	0.4	0.3	1.2
<i>Mantella harolämeieri</i>																					
ZFMK 25351	M	HI	22.0	6.8	8.6	2.4	1.4	1.8	1.4	14.4	6.3	34.8	16.0	10.9	1.5	0.85	0.43	0.83	0.38	0.38	6
ZFMK 21805	F	PT	26.8	7.5	10.8	2.6	1.9	2.0	1.5	16.2	6.8	37.2	16.7	10.9	1.7						3
ZFMK 21806	M	PT	23.1	7.0		2.5	1.3	1.8	1.4	13.8	6.0	33.4	15.9	10.6	1.4	0.88	0.53	0.58	0.48	0.25	6
ZFMK 21807	M	PT	21.4	7.2	8.4	2.4	1.4	2.1	1.3	14.0	6.2	33.4	16.4	10.1	1.5						6
ZFMK 25352		PT	22.7	7.0	8.7	2.5	1.4	1.9	1.3	14.5		34.3	16.0	10.3	1.5						6
ZFMK 25353		TOI	24.0	7.0	8.2	2.4	1.4	1.9	1.3	15.7	6.5	35.5	16.3	10.3	1.4						6
<i>Mantella nigricans</i>																					
MNHN 1973 555	F	IT	26.3	7.5	10.4	2.8	1.6	1.9	1.7	17.1	7.3	39.1	18.8	12.3	1.9	1.0	0.5	0.9	0.5	0.5	5
<i>Mantella bernhardi</i>																					
ZFMK 5/164	M	HI	19.0	5.9	8.0	2.2	1.1	1.7	1.2	12.7	5.1	29.1	13.5	8.6	1.4	0.50	0.33	0.65	0.53	0.23	5
<i>Mantella madagascariensis</i>																					
MNHN 1895 276		LT	21.8	6.8	8.4	2.3	1.3	1.9	1.7												
MNHN 1895 277		PLT	17.9			2.2	1.2						13.8	8.9							
<i>Mantella lopesi</i> (syn. <i>Mantella madagascariensis</i>)																					
MNHN 1935 416		PT	28.6	8.4	10.7	3.1	1.8	1.9	1.8	16.3	6.8	39.6	18.7	12.6	1.5	0.76	0.60	1.30	0.95	0.85	2
<i>Mantella pulchra</i>																					
BMNH 1947 2 7 20		HI	24.7	7.5	10.3	2.4	1.4	1.9	1.8	15.8	6.6	34.9	16.2	10.9	1.8	0.7	0.5	1.4	0.6	0.6	4
BMNH 1947 2 7 27		TOI	24.7	6.9	9.6	2.5	1.4	1.8	1.6	15.3	6.6	34.8	16.6	10.8	1.9	0.4	0.3	1.3	0.65	0.6	1-2
BMNH 1947 2 7 28		TOI	26.0	7.4	10.7	3.0	1.5	1.8	1.6	15.2	6.0	33.8	16.5	11.0	1.7	0.5	0.4	1.5	0.7	0.3	1.2
BMNH 1947 2 7 29		TOT	24.3	7.1	9.2	2.3	1.7	2.0	1.6	14.5	5.9	32.7	15.6	9.8	1.5	0.7	0.5	1.3	0.5	0.3	3
BMNH 1947 2 7 30		TOT	25.0	7.4	9.9	2.6	1.5	1.8	1.3	15.7	6.1	33.5	15.6	10.3	1.4	0.45	0.35	1.6	0.7	0.5	1-2
BMNH 1947 2 7 31		TOT	21.9	7.2	8.9	2.5	1.4	1.8	1.6	14.3	5.9	31.9	15.5	10.0	1.5	0.5	0.4	1.2	0.7	0.6	3
ZMB 50105		TOT	23.1	6.8	9.1	1.9	1.3	2.1	1.3	13.6	5.2	32.0	16.2								
ZMB 30576		TOT	24.5	7.9	10.0	2.7	1.7	1.8	1.3	15.1	6.7	35.1	17.0	11.7	1.4	0.63	0.43	1.28	0.45	0.43	1
MNHN 1991 2843		TOT	23.9	7.7	10.4	2.8	1.6	2.4	1.7	15.3	6.5	37.2	16.7	11.4	1.5	0.55	0.45	1.50		0.50	3
MNHN 1928 106		TOT	24.8	7.3	10.1	3.2	1.4	1.9	1.8	14.8	6.3	33.2	16.0	10.4	1.4						3

Collection number	Sex	Sist.	SVL	HW	HL	Eye	Tym	Fye-Ns	Ns St	Toe1	HaL	HiL	FoTL	FoL	ToL1	DW3	FW3	IMTL	IMTB	IMTH	TT
<i>Mantella aurantaca</i>																					
MNHN 1899 412	M?	LT	21.2	6.0		1.9	1.1				5.5	32.4	15.4	10.2							5
MNHN 1899 413	F	PLT	20.8	5.7		1.9	1.2				5.5	31.0	14.2	9.4							
<i>Mantella aurantaca rubra</i> (syn. <i>Mantella aurantaca</i>)																					
ZFMK 68Ro8	F	LT	24.6	7.8	9.6	2.6	1.6	2.0	1.6	14.1	5.6	31.5	15.2	9.9	1.5	0.6	0.5	0.8	0.6	0.5	3
<i>Mantella crocea</i>																					
ZFMK 45007	F	HT	22.5	6.9	9.4	2.7	1.3	1.6	1.4	13.5	5.6	30.7	14.4	9.7	1.5	0.58	0.40	0.68	0.53	0.40	3
ZIMK 45008		PT	19.3	5.8	8.0	2.1	1.3	1.2	0.9	12.2	5.1	27.6	12.9	7.9	1.4						5
ZFMK 50173		PT	22.0	6.0	8.2	2.0	1.4			13.1	5.4	31.1	14.2	9.6	1.4						3
ZFMK 50174		PT	17.0	5.4	7.7	1.9	1.1	1.4	1.2	11.0	4.4	25.9	12.0	7.7	1.3						5
ZFMK 50175		PT	20.2	6.2	8.7	2.2	1.3	1.8	1.0	1.8	4.9	29.4	13.4	8.8	1.5						5
ZFMK 50176		PT	21.1	6.2	8.3	2.2	1.4	1.6	1.2	12.9	5.4	29.7	14.2	9.0	1.4						3
ZIMK 50177		PT	19.9	5.7	7.8	2.0	1.1	1.6	1.0	13.3	5.6	29.4	14.2	8.9	1.2						5
ZFMK 50178		PT	22.8	6.2	8.2	1.9	1.2	1.9		13.9	5.2	31.4	14.4	9.0	1.7						3
ZFMK 50179		PT	20.7	6.1	7.9	2.1	1.1	1.6	1.2	12.7	5.2	29.7	13.8	9.0	1.3						4
ZFMK 50180		PT	20.4	5.9	8.0	2.2	1.4	1.4	1.1	13.2	5.5	27.5	13.8	8.9	1.3						4
ZFMK 50181		PT	19.5	5.4	7.4	1.8	1.3	1.6		11.8	5.1	29.0	12.8	8.3	1.0						6
ZFMK 50182		PT	17.5	5.3	7.1	1.7	1.2			11.1	4.8	26.3	12.3	9.0	1.2						5
ZFMK 50183		PT	19.3	5.6	7.5	2.2	1.3	1.5	1.0	11.5	4.6	27.0	12.9	8.7	1.2						4
ZFMK 50184		PT	18.5	5.3	7.2	1.8	1.2	1.6	0.9	11.6	5.4	25.8	13.0	8.5	1.5						5
ZFMK 50185		PT	20.3							13.0		29.0	13.0	8.8							
ZFMK 50186		PT	19.6	5.5	8.5	2.0	1.2	1.3	1.2	13.6	4.9	28.4	13.5	9.0	1.5						
ZIMK 50552		PT	20.9	6.0	8.4	2.2	1.3			13.2	5.5	30.7	14.8	9.3	1.5						3
ZIMK 50553		PT	20.8	6.0	7.9	2.2	1.3	1.5	1.2	13.7	6.4	30.7	14.2	8.8	1.4						6
ZFMK 50721		PT	23.0	6.7	8.1	2.5	1.5	1.9	1.2	13.4	5.8	29.8	14.5	9.3	1.6						3
ZFMK 50722		PT	22.4	6.2	7.8	2.0	1.1			13.4	5.6	31.4	15.1	9.8	1.2	0.48	0.33	0.68	0.38	0.10	3
ZFMK 50723		PT	17.4	5.1	6.8	1.8	1.1	1.2	1.1	9.6	4.0	24.0	11.1	7.0	0.9						5
ZIMK 50724		PT	22.9	6.4	9.5	2.4	1.4	1.7	1.2	14.5	5.5	30.9	14.7	9.7	1.7	0.45	0.30	0.55	0.45	0.25	3
ZFMK 50725		PT	20.4	6.1	8.5	2.3	1.2	1.4	1.1	13.3	5.2	29.6	13.8	9.2	1.6						5
<i>Mantella milotympanum</i>																					
ZFMK 65626	M?		22.4	6.4	9.6	2.7	1.7	1.6	1.3	14.4	6.3	31.4	14.7	10.1	1.6	0.5	0.3	0.8	0.5	0.5	3

Diagnosis (1) *Morphology*: The smallest known *Mantella* SVL 19-22 mm, males 19 mm, females 19-22 mm. TTA reaching the posterior eye margin or the eye center. Terminal disks of fingers and toes slightly expanded. Tympanum/eye ratio generally 1/2 to 3/5. IMT small (ratio width/length more than 4/5). – (2) *Dorsal color and pattern*: Dorsum and head dark grey or brown. A fine light middorsal line sometimes present. Flanks black Poorly contrasted dorsolateral color border. No frenal stripe. Humerus yellowish beige, femur bright yellow, this color extending slightly onto the flanks as small flank blotches. Fibula and hands, as well as tibia and feet, brown with generally only one distinct dark crossband, respectively. No flashmarks, but posterodorsal part of femur and knee hollow orange as ventral surface of hindlimb. Iris with light pigment in its upper part (3) *Ventral color and pattern*: Venter, throat and forelimbs black with few large whitish blue markings which can be irregularly vermiculated, but always with very distinct, largely rounded borders. Throat with a distinct horseshoe marking, often covering most of the throat surface in males, being smaller and sometimes not continuous in females. Tibia and femur orange. Foot and tarsus are also orange, but this color is mostly covered by irregular dark pigment.

Mantella madagascariensis group

Mantella madagascariensis (Grandidier, 1872)

- Dendrobates madagascariensis* Grandidier, 1872 *Name-bearing type* lectotype, by designation of GLAW & VENCES (1994: 403), MNHN 1895 276, sex unknown due to bad preservation, SVL 21.8 mm *Type locality*: "Forêt d'Ambalavato, entre Mananjary et Fianarantsoa" according to the original description, given as "forêt d'Ambalavato, entre Mananjary et Fianarantsoa" by BLOMMERS-SCHLÖSSER & BLANC (1991) *Other types*: paralectotype, following lectotype designation of GLAW & VENCES (1994), MNHN 1895 277 – *Etymology*: named after its geographic origin, Madagascar
- Mantella madagascariensis* WERNER, 1901, MOCQUARD, 1909, BOULENGER, 1882, BUSSE, 1981 (part.), PINTAK, 1990 (part.), BLOMMERS-SCHLÖSSER & BLANC, 1991 (part.), GLAW & VENCES, 1992a (part., see localities), 1994 (part., see localities), HERRMANN, 1993 (fig.), STANISZEWSKI, 1997a (fig. p. 12); LARSEN, 1997 (fig.); VENCES & KNIEL, 1998
- Mantella m. madagascariensis* MEIER, 1986 (fig. 5)
- Mantella loppesi* ROUX, 1935 *Name-bearing type* holotype as inferred from original description (ROUX, 1935: 441; see comment below), NMB 4849, female and sex according to FORCART (1946) *Type locality*: "Moroulambo, province de Vatomaniry", according to the original description *Other types*: two paratypes according to original description, one corresponding to MNHN 1935 416, and the second specimen probably stored in the La Rochelle Museum (see comment below) *Etymology*: named after E. LOPPÉ, former director of the La Rochelle Museum
- Mantella loppesi* FORCART (1946), BUSSE, 1981 (syn. *madagascariensis*), BLOMMERS-SCHLÖSSER & BLANC, 1991 (syn. *madagascariensis*)
- Mantella "loppi"* GLAW & VENCES, 1994, STANISZEWSKI, 1997b (fig. p. 57)
- "*Mantella nasuta* sp." [nomen nudum, referring to the "variable" color morph] CLARK, 1994 (fig. p. 10 above and p. 11 above).
- Mantella* sp. [referring to the "variable" color morph] CLARK, 1994 (fig. p. 11 below), VENCES et al., 1994 (fig. p. 391), GLAW & VENCES, 1994 (plates 58-60)
- "*Mantella mysteriosa*" [conditional name, referring to the "variable" color morph] BARTLETT, 1995 (fig. p. 18)
- Other chrysonyms
- Mantella pulchra*: GLIBÉ, 1964, 1978 (part.)
- Mantella covani*: WOLPERT & MÜLLER, 1980
- Mantella crocea* BARTLETT, 1995 (fig. p. 16 below) [referring to the "variable" color morph]

Identity: Dorsal color patterns of this species are sometimes very similar to *M. baroni*, and single specimens can only be identified by combination of several color characters. The

syntopic occurrence of *M. baroni* and *M. madagascariensis* as recorded by us in Vohiparara, however, demonstrates that both must be regarded as separate species. As far as can be concluded from large series of specimens exported from Madagascar in the pet trade, the pattern is constant at some localities but may be extremely variable elsewhere.

M. madagascariensis was considered as "nomen dubium" by several authors based on the very bad state of preservation of the types and the short and little detailed original description (GUIBE, 1964; DALY et al., 1996). A detailed examination of the lectotype, however, revealed one character which is still recognizable and can be used for a diagnosis. The specimen's dorsal and ventral color has nearly completely faded to uniform brownish. The hindlimbs are separated from the body. The posteroventral part of the femur and the distal part of the tibia, in the knee hollow area, still show some contrasting pattern with an extension corresponding exactly to the flashmarks present in all specimens of the form here attributed to *M. madagascariensis* (see fig. 11). Ventrally, the lectotype shows light color extending onto the distal part of the femur, corresponding to the pattern generally present in the form here attributed to *M. madagascariensis* but not in the otherwise rather similar *M. pulchra* (fig. 12).

Comments. (1) The paralectotype of *M. madagascariensis* is most probably a subadult, but it may also be a *M. bernhardi* and thus not conspecific with the lectotype. (2) Status of two names coined in recent publications to refer to "variable color morphs" must be discussed here. "*Mantella mysteriosa*" was used in quotation marks by BARTLETT (1995). The author states explicitly (p. 20) that this name originated from a pet dealer's list. Diagnosis, type designation and type locality were not given. The name must thus be seen as documentation of the usage of a conditional name in the pet trade, and is not nomenclaturally available. "*Mantella nasuta* sp." was used by CLARK (1994) in the captions of two figures. No unequivocal diagnosis of the specimens figured is possible since neither dorsal pattern of hindlegs nor ventral coloration were documented or described. Further diagnosis, type designation and type locality were not given. No direct reference to the name is to be found in CLARK's (1994) text and key. Two common names, Mimic Mantella and Panther Mantella, are used in the captions of the figures on p. 10-11 to refer to specimens named *Mantella nasuta* sp. Both common names were also included in CLARK's (1994) species list as "*Mantella* sp. A" and "*Mantella* n. sp. 5". The latter two names, on the other hand, are also found in his key. Thus, two forms considered as different species are indirectly keyed as *M. nasuta* sp., and there is no direct diagnosis related to this name, which we consider as a nomen nudum. - (3) *Mantella loppet*, according to the original description (ROUX, 1935), was based on "3 Amphibiens appartenant au genre *Mantella* et qui représentent une espèce nouvelle M le Docteur Et. Loppé a bien voulu nous autoriser a conserver pour le Musée de Bâle le spécimen-type de l'espèce, tandis que deux autres exemplaires se trouvent au Musée de La Rochelle." Although not explicitly mentioned, this infers the existence of a holotype in the collection of the Basel Museum (NMB 4849 according to FORCART, 1946), and two additional specimens which we consider as paratypes (originally both in the La Rochelle Museum; one later exchanged with the Paris Museum, catalogued as MNHN 1935.416).

Material examined. NMB 4849 (Prov. Vatamandry, Mouroulambo, coll. E. PICHON 1930) MNHN 1895 276-7 (Ambalavato, lectotype and paralectotype), MNHN 1931 12 (Moramanga), MNHN 1931 13 (Moramanga), MNHN 1935 416 (Vatamandry, J. ROLX, "don du DR. LOPPE, Conservateur du Musée de la Rochelle", paratype of *M. loppet*), MNHN 1992 4821-2, MNHN 1993 1440, MNHN 1993 1445

(origine inconnue); ZFMK 14184-207 (Niagarakely; leg. H. MEIER 1972; 14186, 14188, 14196·CS), ZFMK 14209-13 (Niagarakely; leg. H. MEIER 1972); ZFMK 14325-30 (Niagarakely, leg. H. MEIER 1974); ZFMK 14471-5 (Niagarakely; leg. H. MEIER 1973); ZFMK 22107-12 (Niagarakely; leg. H. MEIER 1973); ZFMK 56153-4 (pet trade; ded. F. GLAW XI.1993), ZFMK 60132 (locality unknown, ded. F. GLAW IV.1995, ZFMK 62740-1 (locality unknown, CS); ZFMK 62732-6, ZFMK 62738-9 (locality unknown, TE), ZFMK 62737 (locality unknown, TE, pattern very similar to *M. baroni*), ZFMK 64138 (Vohiparara, leg. F. GLAW, D. RAKOTOMALALA & F. RANAIVOJANA III.1996; TE).

Distribution. – Type locality is [1] Ambalavato near Ranomafana. Type locality of the junior synonym *M. loppet* is [2] Marolambo (Vatomandry). ZFMK vouchers were collected at [3] Niagarakely. At [4*] Vohiparara (ca. 1000 m altitude, near Ranomafana), we found one specimen syntopic with *M. baroni*. According to A. PEYRIERAS (personal communication), populations of the “variable morph”, here included in *M. madagascariensis*, occur near [5] Beparasy. See the discussion in the section on the distribution of *M. baroni*.

Diagnosis. – (1) *Morphology:* A medium-sized *Mantella*. Compared with *M. baroni*, general body shape rather stout. SVL 20-27 mm, recorded lengths of males 21-22 mm, of females 24-25 mm. TTA rarely reaching the eye center, sometimes the posterior eye margin, mostly the tympanum, and sometimes only the forelimb insertion. Terminal disks of fingers and toes slightly expanded. Tympanum/eye ratio generally 1/2 to 3/5. IMT large (ratio width/length less than 3/5). – (2) *Dorsal color and pattern:* Upper head surface, dorsum and flanks black, generally without recognizable dorsolateral color border. Yellowish rostral stripe present. Femur and humerus yellow to green, this color extending as large flank blotches onto the flanks and sometimes onto the dorsum. Distinct orange flashmarks present. Tibia, tarsus and foot orange with or without blackish crossbands and marblings. Iris mostly containing light pigment in its upper part. Rostral stripe often in contact with flank blotch. In specimens of the “variable morph”, yellow color in varying extension can sometimes be present on the dorsum. All intermediate states, from a few yellow spots to a reticulated yellow marbling or a dense yellow speckling, are known. A greenish frenal stripe, often interrupted, can be present as well. Specimens without reliable locality information are known which are nearly uniformly yellow dorsally and ventrally, with only a few blackish spots and marblings. In these specimens, the more distinct yellow surface in the flank blotch area is reminiscent of the typical coloration, but it is not clear whether they really are conspecific with *M. madagascariensis*. (3) *Ventral color and pattern:* Venter, throat and forelimbs black with light markings (mostly whitish-blue, sometimes yellow to green), these being generally rather large, rounded, and situated posteriorly on the venter. Distinct horseshoe marking present, more extended in males. Femur, tibia (except flashmark area), tarsus and foot often uniformly orange, in other specimens with areas of black and yellow (the latter corresponding to yellow color on the dorsal surface). Areas of femoral “glands” often darkly pigmented. In some specimens, femur nearly totally black with blue spots. In “variable” specimens, typical ventral pattern sometimes replaced by a dense yellow marbling.

Mantella pulchra Parker, 1925

Mantella pulchra Parker, 1925. *Name-bearing type* holotype by monotypy, BMNH 1947.2.7.20 (ex 1925.7.2.58), female according to original description, SVL 24.7 mm. *Type locality:* “Antsahanaka” according to original description. *Other types:* none (see comment below). *Etymology:* derived from Latin *pulcher* (beautiful).

Mantella pulchra: GUIBÉ, 1964, 1978 (part); GLAW & VENCES, 1994; HENKEL & SCHMIDT, 1995 (fig. p. 56), BARTLETT, 1995 (fig. p. 24 above left), VAN TUJL, 1995, CARISSIMI PRIORI, 1995 (fig. p. 43), STANISZEWSKI, 1996 (pl. p. 23), 1997b (fig.), 1998a (fig.), DALY et al., 1996; LARSEN, 1997; VENCES & KNIEL, 1998

Other chrysonyms.

Mantella madagascariensis DALY et al., 1984; BLOMMERS-SCHLÖSSER & BLANC, 1991 (part)
Mantella madagascariensis madagascariensis BUSSE, 1981 (part.).
Mantella sp. cf. *madagascariensis* GARRAFFO et al., 1993
Mantella madagascariensis (colour morph *Mantella "pulchra"*): GLAW & VENCES, 1992a
Mantella cowani pulchra. ANDREONE, 1992, GAVETTI & ANDREONE, 1993 (p. 105).
Mantella cowani. ZIEGENHAGEN, 1981, LE BERRE, 1993 (inner fig. on p. 21).
Mantella sp.: STANISZEWSKI, 1998a (fig.).

Comments. – (1) According to the BMNH catalogue, there were 22 “paratypes” (old numbers BMNH 1925 7.2.59-80), one of which (ex BMNH 1925 7.2.80) was cleared and stained and seemingly not given a new number when the types were re-numbered in 1947. Nine additional specimens were exchanged according to this catalogue. Seven of these were located by us: MNHN 1928.106, MNHN 1991.2843 (ex MNHN 1928.106.A), ZMA 5809-10 (according to VAN TUJL, 1995), ZMB 50105, ZMB 30576, MZUT An 108 (all from Antsihanaka). According to VAN TUJL (1995), “paratype(s)” were also deposited in the MCZ collection. (2) The original description of *M. pulchra* was based on a single specimen (“Type specimen: a female from Antsihanaka”; PARKER, 1925: 394), and contains no mention of other specimens. Although the specimens listed above have similar collecting dates as the holotype, they can therefore not be considered as paratypes. As already stated by GAVETTI & ANDREONE (1993), they must be regarded as topotypes only.

Material examined. – BMNH 1947 2 7 20-32 (holotype and paratypes; all from Antsihanaka, coll. or purch. ROSENBERG), MNHN 1928 106, MNHN 1991 2843 (“acquis par échange avec le British Mus. [Nat. History] en 1927”, paratypes), MNHN 1993 1443 (locality unknown), ZFMK 52122-3 (locality unknown; ded. D. KARBE 1991); ZFMK 56155 (locality unknown; ded. F. GLAW XI, 1995, CS), ZFMK 62258 (An’Ala bei Andasibe; leg. F. GLAW 3 II 1996), ZFMK 62742-4 (locality unknown, CS), ZFMK 62645-59 (locality unknown; TEJ); ZMB 50105, ZMB 30576 (Antsihanaka, exchanged with BMNH in III 1927, paratypes), MRSN A0059 1-4 (An’Ala [syntopic with *M. baroni*]; leg. F. ANDREONE 4.I 1992 [sacrificed 14 XI 1992]); MRSN A444.1-3 (locality unknown), TM 9893, TM 9897, and possibly the juvenile TM 9901 (Folohy, coll. METHUEN)

Distribution. Type locality is [1] Antsihanaka. ANDREONE (1992) and DALY et al. (1996) collected the species near [2*] An’Ala (near Andasibe; ca. 850-1000 m altitude), and A. PEYRIERAS (personal communication) in [3] Andekaleka (Rogez). Further localities within the [4] Mananara reserve (ca. 100-200 m altitude) were published by DALY et al. (1996). Specimens in the TM corroborate the occurrence in [5] Folohy. Exact location of the type locality Antsihanaka is unknown; most probably, it was used in the past for a forested region near Lake Alaotra (see VIETTE, 1991). BLOMMERS-SCHLÖSSER & BLANC (1991, map 4) locate Antsihanaka, probably erroneously, east of Andasibe.

Diagnosis. – (1) **Morphology.** A medium-sized *Mantella*. General body shape rather stout. SVL 21-25 mm, recorded length of males 22-23 mm. TTA often reaching the posterior eye margin, sometimes the tympanum or the forelimb insertion. Terminal disks of fingers and toes slightly expanded. Tympanum/eye ratio generally less than 3/5. IMT very large and protruding (ratio width/length less than 1/2). – (2) **Dorsal color and pattern.** Dorsum and flanks dark brown to black. On the upper head surface, the dark color of the dorsum gradually fading into light brown. Dorsolateral color border present; indistinct in the inguinal

region, but very distinct in the head and shoulder region. Hand, fibula, foot, tarsus and tibia light brown, with few dark brown crossbands. Humerus and femur yellow to green, in some specimens (locality unknown) blue. This color extending as relatively large flank blotches onto the flanks. Flank blotches delimited by the dorsolateral coloration border and not extending onto the dorsum. Bright red flash marks present. Iris with light pigment in its upper part. (3) *Ventral color and pattern*: Venter, throat, forelimbs and femur dark brown to black with small, generally regularly rounded whitish-blue spots and a distinct horseshoe marking, which in males can cover nearly the complete throat. Tibia with a distinct orange marking, sometimes continued on the knee, distal part of femur and foot. In preservative, this coloration changes, becoming partly bright red and partly white, with a sharp border between both colorations (see also DALY et al., 1996). A similar but less distinct change is also observed in specimens of *M. madagascariensis*.

Mantella aurantiaca group

Mantella aurantiaca Mocquard, 1900

Mantella aurantiaca Mocquard, 1900a - *Name-bearing type* lectotype, by present designation, MNHN 1899 412, probably a male, SVL 21.2 mm. *Type locality* "une forêt entre Beforona et Moramanga". according to the original description. *Other types* paralectotype, following present lectotype designation, MNHN 1899 413 - *Etymology*, derived from Latin *aurantiacus* (golden).

Mantella aurantiaca MOCQUARD, 1900b, 1909, WERNER, 1901, METHUEN & HEWITT, 1913, GÜLBÉ, 1964, 1978, AUDY, 1973, MUDRACK, 1965, 1974, ARNOULT, 1966, MATZ, 1975 (fig.), BACHMANN & BLOMMERS-SCHLOSSER, 1975, BLOMMERS-SCHLOSSER, 1978, 1979a, OOSTVEEN, 1978a-b, MLEFR, 1980 (fig. p. 353 above), 1986, BISSÉ, 1981, DALY et al., 1984, 1996, 1997a, UNFRIED, 1987, VAN TOMME, 1988 (fig. 1); AMMER, 1989, SIGENTHALER, 1989, PINTAK, 1990, OLIVETTI, 1990 (fig.), BLOMMERS-SCHLOSSER & BLANC, 1991, PRESTON-MAFHAM 1991 (fig. p. 79), ANDREONE, 1992 (pl. III fig. 1 2), GLAW & VINCES, 1992a, 1994 (part), 1998, ZIMMERMANN, 1992, 1996a-b, ZIMMERMANN & ZIMMERMANN, 1992 (fig. 5, 15 16), 1994, LE BERRE, 1993 (fig. p. 21), GARRAFFO et al., 1993, HERRMANN, 1993 (fig.), CLARK, 1994 (fig. p. 7), HAY et al., 1995, BARTLETT, 1995 (fig. p. 18 below left), HENKEI & SCHMIDT, 1995 (fig. p. 49), CARISSIMI PRIORI, 1995 (part fig. p. 41 above and below right), STANISZEWSKI, 1996 (pl. p. 23 and 26), 1997a-b (fig.), 1998a (fig.), 1998b, LARSEN, 1997; PINTAK et al., 1998, VENCLES & KNIEL, 1998

Mantella aurantiaca rubra Staniszeowski, 1996 - *Name-bearing type* lectotype, by present designation, ZFMK 68868, female, SVL 24.6 mm. *Type locality* origin of lectotype unknown, taxon is said to occur in "forests of Anosibe An'Ala" according to original description. *Other types* an unspecified number of (probably lost) paralectotypes. - *Etymology* derived from Latin *ruber* (red)

Mantella aurantiaca rubra STANISZEWSKI, 1997b (fig.)

Identity. - *Mantella aurantiaca* is one of the early names in the genus, and its status as a distinct species has never been questioned

Comments. (1) The lectotype specimen of *M. aurantiaca* is probably a male, with longitudinal, lateral cuts on both sides on the body, and is in slightly better state of preservation than the paralectotype. The paralectotype is a female in rather poor state of preservation, with a longitudinal cut through the ventral skin. (2) STANISZEWSKI (1996) coined the name *Mantella aurantiaca rubra* for specimens with a red (instead of yellowish-orange) color. His diagnosis, although very short, gives in words one character (color) and should thus be recognized as valid according to the Code. "The type orange form is located in *Pandanus*

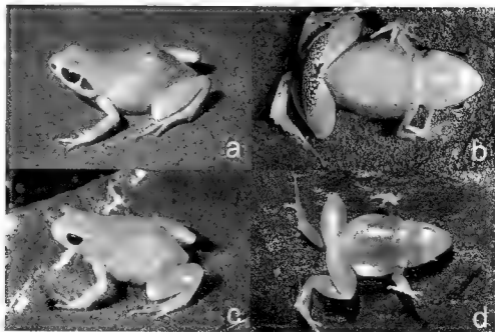


Fig 3 - Photographs of *Mantella* species. (a-b) *M. milotympanum*, specimen without locality data (ZFMK 65626), dorsolateral and ventral view, (c-d) *M. aurantiaca*, specimen without locality data, reddish morph (ZFMK 65627), 1997, dorsolateral and ventral view

forests around Andasibe [.] and the deep blood orange form [known as *M. a. rubra*] in the forests of Anosibe An'Ala." No figure was published together with this description, but several color photographs were published later (STANISZEWSKI 1997b, 52-53) by the same author. The assumed type locality Anosibe An'Ala given by STANISZEWSKI (1996) was probably based on GLAW & VENCES (1994), but STANISZEWSKI's captive specimens (including the lectotype described below) almost certainly were obtained through the pet trade without locality; consequently, the taxon *rubra* has currently no type-locality. (3) Regarding the validity of *rubra*, it must be stressed that, according to several authors (e.g. ZIMMERMANN & ZIMMERMANN, 1994, DALY et al., 1996), reddish *aurantiaca* morphs occur at several localities, parapatrically with more orange populations. No evidence supports the status of *rubra* as valid subspecies or species, and no genetic differences were found by allozyme electrophoresis between reddish and orange-colored *aurantiaca* specimens (M. VENCES, personal observation), we consider *rubra* as synonym of *M. aurantiaca*.

Description of the lectotype of Mantella aurantiaca rubra Staniszeowski, 1996 ZFMK 68868, adult female with developing oocytes, supplied by M. STANISZEWSKI in 1998 and said to belong to the series on which the original description was based. Specimen in good state of

preservation with a longitudinal cut through right flank. For measurements see tab. 2. Body rather stout; head not broader than body; snout rounded in dorsal and lateral view; nostrils directed laterally, not protuberant, nearer to tip of snout than to eye; canthus rostralis weak, straight; loreal region plain; tympanum rather indistinct, medium-sized, rounded, its diameter about half of eye diameter; supratympanic fold weakly developed, tongue ovoid, only very slightly bifid posteriorly; maxillary and vomerine absent; choanae small, rounded. Arms moderately slender, subarticular tubercles single; outer metacarpal tubercle rounded, inner metacarpal tubercle elliptical, both very weakly developed; fingers without webbing; finger length $1 < 2 < 4 < 3$, finger 4 only slightly longer than 2; finger 2 only slightly longer than 1; terminal finger disks nearly not developed. Legs moderately robust; tibiotarsal articulation reaching tympanum; feet with small, rounded inner and outer metatarsal tubercles, subarticular tubercles single, rounded; toe disks nearly not developed. Foot without webbing. Lateral metatarsalia connected; toe length $1 < 2 < 3 < 5 < 4$, toe 3 distinctly longer than 5. Skin on the dorsal and ventral surface smooth. Color in life unknown; in preservative uniformly orange, ventrally translucent orange. Flashmarks visible as yellowish areas. Iris black, pupil whitish (due to fixation).

Material examined - BMNH 1953.1.5 40-41 (Madagascar, pres. G. W. ALLAN), BMNH 1956.1.1.13 ([6 specimens NIL] Périnet District, L. MASON), MNHN 1899 412-3 (lectotype and paralectotype, forest between Beforona and Moramanga), MNHN 1953 137 (Périnet, forêt), MNHN 1984 117-23 (coll. RAZARIHELISOA), MNHN 1988 751.5-25 (pet trade); MNHN 1993 1435-9 (locality unknown), MNHN 1994.1105-10, ZFMK 22113-22 (Périnet; leg. H. MEIER 1973, 22113, 22115, 22119. CS); ZFMK 56170-83 (locality unknown, ded. F. GLAW XI 1993), ZFMK 62776, ZFMK 62779, ZFMK 62780, ZFMK 62783, ZFMK 62785 (locality unknown; TE); ZFMK 62774, ZFMK 62777 (locality unknown; TE; live coloration orange), ZFMK 62775, ZFMK 62778, ZFMK 62781-2, ZFMK 62784 (locality unknown; TE; live coloration reddish), ZFMK 68868 (locality unknown, lectotype of *M. a. rubra*, ded. M. STANISZEWSKI, 1998).

Additional specimens were not examined in detail, they are here listed according to the catalogue entries: MNHN 1976 235-6, MNHN 1976 240-2 (locality unknown), MNHN 1976 237 9 (forêt de Périnet [239 tadpoles according to catalogue]), MNHN 1976 243-9 (forêt de Périnet), ZFMK 8861-70 (Périnet, leg. H. MEIER 1973); ZFMK 9127-35 (Périnet, leg. H. MEIER III 1973), ZFMK 13648-9 (Périnet, leg. H. MEIER 1972), ZFMK 14700 (Périnet, leg. H. MEIER XI 1974), ZFMK 14331-6 (Périnet, leg. H. MEIER II 1974); ZFMK 50170-2 (Andasibe [Périnet], leg. H. MEIER II 1989), ZFMK 51792 (Andasibe [Périnet], leg. F. W. HENKEL et al. 1988/89), MRSN A0736 1-4 (locality unknown, through the pet trade), MRSN A0060 1-4 (Périnet [?], leg. F. ANDREONE 24 IV 1990), TM 10047 50, 10053-5, 10057-59 (Ambatoharanana, coll. P. A. Methuen [TM 10051, 10052, 10056 exchanged with MCZ]).

Distribution - Occurrence in Andasibe is often quoted, but most probably the species does not occur in the immediate vicinity of this village, records referring to single introduced specimens. ZIMMERMANN & HETZ (1992) and ZIMMERMANN & ZIMMERMANN (1994) mapped *M. aurantiaca* localities in the area of the Torotorofotsy swamps NW of Andasibe. They found several (more or less isolated) populations, mainly in the northern part of the swamp, one of these consisting mainly of red colored specimens.

Localities are [1*] the Torotorofotsy swamps (including also Antanditra, see BLOMMERS-SCHLOSSER, 1979) and two other localities which are based on a personal communication of A. PEYRILRAS: uniformly yellow or orange *Mantella* specimens are known from near [2] Beparasy, whereas near [3] Anosibe An'Ala reddish specimens occur. METHUEN & HAWITT (1913) reported the species from [4] Ambatodradama (Ambatoharanana according to TM catalogue), which, according to their map, is located near Analamazaotra.

Detailed data on the distribution of the species were also included in the unpublished report of BEHRA et al. (1995). These authors, beside delimiting the exact distribution area in the Torotorofotsy area, listed several other localities of uniformly colored *Mantella* in the central part of the Eastern Region. Considering the existence of another uniformly orange species, *M. milotympanum* (see below), specific belonging of these populations is uncertain. Uniformly orange specimens were also observed on the Rantsara plateau between Ihosy and Ivohibe (A. PEYRIERAS, personal communication). This record, however, possibly corresponds to *M. aff. baroni* which occurs on Pic Ivohibe. The locality "Fihierenana valley" (see GLAW & VENCES, 1994) is here referred to *M. milotympanum* (see below). The map shown by UNFRIED (1987), giving the whole of eastern Madagascar as the distribution area of *M. aurantiaca*, must clearly be considered as pure fantasy.

Diagnosis – (1) *Morphology*. A generally rather small and stout *Mantella* SVL generally 19-24 mm, but some females can reach up to 31 mm. TTA reaching the forelimb insertion in large females, the eye center in small specimens, but generally the tympanum or posterior eye margin. Terminal disks of fingers and toes slightly expanded. Tympanum/eye ratio between 1/2 and 3/5. IMT medium sized (ratio width/length slightly less than 3/4) – (2) *Dorsal color and pattern*: Uniformly yellow-orange, in some populations red-orange, often with a translucent shade. Bright red flashmarks present. Iris nearly uniformly black, only a little light pigment in its upper part. – (3) *Ventral color and pattern*: Uniform, similar to dorsal surface but generally somewhat lighter, except red flashmark (extended nearly on the whole tibia). Some inner organs visible through the slightly transparent ventral skin.

Mantella crocea Pintak & Bohme, 1990

Mantella crocea Pintak & Böhme, 1990 – *Name-bearing t. pe* holotype by original designation (PINTAK & BÖHME, 1990: 59), ZFMK 45007, female, SVL 22.5 mm. *Type locality*: 'Andasibe (= Périnet), mittleres Ostmadagaskar', according to original description. *Other types*: paratypes, ZFMK 45008, ZFMK 50173-86, ZFMK 50552-3, ZFMK 50721-5, and 10 (lost) additional paratypes (see comment below). *Etymology*: derived from Latin *croceus* (saffron yellow).

Mantella crocea PINTAK, 1990, BLOMMERS-SCHLÖSSER & BLANC 1991 (p. 274), ZIMMERMANN, 1992, ANDREONE, 1992 (pl. IV fig. 3-4), GLAW & VENCES, 1992a, ZIMMERMANN & ZIMMERMANN, 1992 (fig. 5.23), OTTENSCHMANN, 1993, GARRAFFO et al., 1993, HERRMANN, 1993 (fig.); ZIMMERMANN & ZIMMERMANN, 1994; GLAW & VENCES, 1994; BARTLETT, 1995 (fig. p. 16 above), HENKEL & SCHMIDT, 1995 (fig. p. 51), ZIMMERMANN, 1996a-b, STANISZEWSKI, 1996 (pl. p. 18 and 23); DALY et al., 1996; STANISZEWSKI, 1997a-b (fig.), 1998a (fig.), LARSEN, 1997; PINTAK et al., 1998, GLAW & VENCES, 1998.

Other chresonyms

Mantella viridis. STANISZEWSKI, 1997a (fig. on p. 13 and 17), 1997b (fig. pp. 33, 49, 50), 1998a (fig.)

Comments. (1) Since the holotype was supplied by the pet trade, the exact location of the type locality is uncertain. It seems rather probable, however, that it is roughly in the central eastern rainforest region north of Andasibe (formerly Périnet). (2) In the original description (PINTAK & BÖHME, 1990), beside the catalogued specimens, 10 living uncatalogued specimens were designated as paratypes. No specimens of this captive stock were eventually preserved and catalogued; all these additional paratypes must therefore be considered as lost.

Material examined – ZFMK 45007 (Périnet area [?], through pet trade, 1986, holotype), ZFMK 45008 (Périnet area [?], through pet trade, 1986; paratype), ZFMK 50173-86 (Moramanga, leg. H. MEIER II.1989; paratypes); ZFMK 50552-3 (Moramanga; leg. F. W. HENKEL, W. SCHMIDT & V. MÜLLER V.1989; paratypes); ZFMK 50721-3 (Moramanga, leg. H. MEIER 1989, paratypes), ZFMK 50724-5 (Andasibe [Périnet], paratypes), ZFMK 51480-2 (Andasibe [Périnet], leg. O. PRONK II.1990), ZFMK 51738-42 (Périnet, leg. H. ZIMMERMANN 1989), ZFMK 52746 (Andasibe? [Périnet]; ded. F. GLAW & M. VENECES 1991, CS), ZFMK 62760-1, ZFMK 62763, ZFMK 62766, ZFMK 62769 (locality unknown, TE); ZFMK 62765, 62767 (locality unknown; TE; live coloration yellow, 62767 CS), ZFMK 62762, ZFMK 62764, ZFMK 62768 (locality unknown, TE, live coloration green); MNHN 1993 1448 (locality unknown); MRSN A0058 (Andasibe [?]; leg. F. ANDREONE 4.I.1992).

Distribution – The type locality (Andasibe) could not be confirmed by recent surveys (see above). Also the Moramanga locality (ZFMK vouchers) seems rather dubious. The only reliable information of which we are aware is included in BEHRA et al. (1995), who confirmed the occurrence of the species in the Bakozetra area north of Andasibe (located immediately to the north of the known distribution area of *M. aurantiaca* in the Torotorotsy swamps).

Diagnosis (1) *Morphology*: A small *Mantella*. Small specimens of slender appearance, large specimens rather stout. SVL 17-24 mm, females 23-24 mm. TTA mostly reaching the tympanum or posterior eye margin, rarely the eye center. Terminal disks of fingers and toes expanded. Mean tympanum/eye ratio nearly 3/5. IMT medium sized (ratio width/length slightly more than 2/3) – (2) *Dorsal color and pattern*. Head, dorsum and posterior part of flanks yellow, orange or light green, sometimes (mainly in the yellowish specimens) with fine black spots. Sometimes an indistinct dark middorsal line and traces of a diamond marking. Head laterally, and anterior flanks generally black (black pattern can be largely reduced in some specimens), with a sharp dorsolateral color border. Light frenal stripe present, often interrupted in the yellowish specimens. Bright red flashmarks present. Iris with some light pigment in its upper part.

(3) *Ventral color and pattern*. Black with a variable number and extension of grey to bluish-white or yellowish markings, sometimes fusing to form an irregular network. Horseshoe marking present and mostly distinct, but poorly developed in some specimens. Hindlimbs sometimes uniformly orange or reddish ventrally, except the red ventral flashmark extension on the tibia. In other specimens, orange color only present on tibia (except flashmark area); foot, tarsus and femur being black with grey-whitish markings. Pictures of dorsal and ventral coloration of the different morphs were given in GLAW & VENECES (1998).

Mantella milotympanum Staniszewski, 1996

Mantella aurantiaca milotympanum Staniszewski, 1996. *Name-bearing type* lectotype, by present designation, specimen figured on p. 18 of STANISZEWSKI (1996), this specimen was not preserved and must therefore be considered as lost (STANISZEWSKI, personal communication). *Type locality*, the taxon is said to occur in the "Fihirenana Valley in central east Madagascar" according to the original description, but the locality of the lectotype is unknown. – *Other types*: an unspecified number of (probably lost) paralectotypes. – *Etymology*: probably derived from classical Greek *melis* (genitive *melanos*), black (*milo* being a derived spelling which possibly was originally created by pet dealers) and classical Greek *tympanum* (Latinized as *tympanum*), drum (meaning eardrum), referring to the black tympanum color.

Mantella aurantiaca milotympanum, STANISZEWSKI, 1997a (fig.)

Mantella aurantiaca "milotympanum": STANISZEWSKI 1997b (fig.)

Mantella "milotympanum", LARSEN, 1997

Other chresonyms

- Mantella aurantiaca* LE BERRE, 1993 (fig. p. 20), GLAW & VENCES, 1994 (part., "black tympanum"),
 CARISSIMI-PRIORI, 1995 (part.; fig. p. 41 below left).
Mantella cf. *aurantiaca*: GLAW & VENCES, 1994 (pl. 52)
Mantella sp. 3 VENCES & KNIEL, 1998.
 "Black-eared mantella": STANISZEWSKI, 1998a.
Mantella sp., Variante 3 GLAW & VENCES, 1998
Mantella sp., Variante 4 GLAW & VENCES, 1998

Identity The name *milotympaanum* was, to our knowledge, first used in a publication by STANISZEWSKI (1996) to name a form of *M. aurantiaca* previously referred to as "black tympanum" variant (GLAW & VENCES, 1994). STANISZEWSKI (in litteris, 1997) had no intention to create a new scientific name, and his paper does not include a formal description nor a type designation. However, it describes distinctive features of the form in a way that must be regarded as a diagnosis:

"I am in no doubt that a mantella currently defined as another subspecies of the golden mantella should be raised to specific status. The black-eared golden mantella (*Mantella aurantiaca milotympaanum*) is so different in appearance and behaviour that it must merit this. [...] The dorsal colour is a slightly drab orange (males brighter than females) while the venter is a greenish yellow (orange yellow in *M. aurantiaca*). This species is overall much slimmer than the golden mantella, the eyes are oblong rather than round and the skin is much more granular. Significant raised veins are apparent on the hind limbs, as its name suggests the eardrum (tympanum) is black as is the nostril region and there is a black line apparent from the eye to the nostril [...]". (STANISZEWSKI, 1996: 24).

According to our observations, the presumed slim habitus is not present in all specimens (especially absent in large females), and the eyes are not of oblong shape (rounded as in other *Mantella*). The presumed "semi-nocturnal behaviour" and "very nervous disposition" were not confirmed by us in our captive group of this species. The same regards the observation of eggs "possessing a yellowish-brown nucleus and measuring only 1 mm in diameter".

Nevertheless, a diagnosis of this form exists (see above), and the name was not used in a conditional way. It must therefore be regarded as nomenclaturally available. Since this form differs from typical *M. aurantiaca* and *M. crocea*, we here consider it as a full species in a preliminary way (see section *Specific status* below).

Comment. The locality information "Fiherenana valley" in the original description almost certainly was based on a personal communication of A. PEYRIERAS as published in GLAW & VENCES (1994). It is not sure that STANISZEWSKI's specimens were collected at this locality.

Lectotype designation We here follow the procedure applied by DLBOIS & OHLER (1997a-b) to stabilize old names for which no type material is preserved in scientific collections but figures were published. The original description (STANISZEWSKI, 1996: 18) includes a color picture which shows all characters currently known as characterizing the form (black pigment on tympanum and around nostril, rather granular skin, dorsal color not of translucent appearance). We designate this figured specimen as lectotype. This specimen (as all specimens kept by M. STANISZEWSKI until the description of *milotympaanum*) was not preserved, and is therefore not available for comparative purposes (STANISZEWSKI, in litteris 1997). A neotype designation is

postponed until specimens with reliable collecting data become available. In the following, we describe one reference specimen from the ZFMK collection for comparative purposes.

Description of reference specimen. – Adult male specimen, ZFMK 65626, SVL 22.5 mm. Specimen in excellent state of preservation, with longitudinal cuts along both flanks. For measurements see tab. 2 Body slender; head not broader than body; snout slightly pointed in dorsal, truncated in lateral view; nostrils directed laterally, not protuberant, nearer to tip of snout than to eye; canthus rostralis weak, slightly concave, loreal region even; tympanum rather indistinct, medium sized, rounded, its diameter about half of eye diameter, supratympanic fold moderately developed, tongue longish, only very slightly bifid posteriorly; maxillary and vomerine absent; choanae small, rounded. Arms slender; subarticular tubercles single; outer metacarpal tubercle rounded, inner metacarpal tubercle elliptical, both very weakly developed; fingers without webbing; finger length $1 < 2 < 4 < 3$, finger 4 only very slightly longer than 2, finger 2 only slightly longer than 1; terminal finger disks nearly not developed. Legs moderately robust; tibiotarsal articulation reaches tympanum, feet with small, rounded inner and outer metatarsal tubercles; subarticular tubercles single, rounded; toe disks faintly developed. Foot without webbing. Lateral metatarsalia connected; toe length $1 < 2 < 3 < 5 < 4$, toe 3 distinctly longer than 5. Skin on the upper surface smooth, slightly granular on the flanks; ventral surface smooth, except for granular thigh patches (“femoral glands”) extending from the anus ca. 5 mm distally (max. width 3.1 mm). Color in life dorsally, and on flanks and upper surface of fore- and hindlimbs deep orange, except for small black areas around the nostril and covering the tympanum. bright red flashmarks. Ventral side orange except for the dirty blackish “femoral gland” region. After one year in preservative, the orange color has changed to olive greenish. The flashmark areas are yellowish. The ventral side is dirty olive except for the hindlimbs which are yellowish. The “femoral gland” region is dark brown with small whitish spots.

Material examined – ZFMK 62770 (locality unknown; CS), ZFMK 62771 (locality unknown, TE), ZFMK 62772, 65626, 68868 (locality unknown; 62772: TE; live coloration red-orange), ZFMK 62773 (locality unknown; TE, live coloration yellow-orange), MNHN 1992.4823 (locality unknown, identification based on remains of dark pigments on tympanum and around nostril).

Distribution According to A. PEYRIERAS (personal communication in GLAW & VENCES, 1994) this species occurs in the Fiherenana valley, located about 50 km N Andasibe (not the Fiherenana valley in the South-Western region, near Tohara).

Diagnosis (1) *Morphology*: Generally, a rather small and stout *Mantella*, although single females can become relatively large. SVL generally 19-23 mm (females exceptionally up to 30 mm, personal observation, specimen not preserved) TTA reaching the tympanum or posterior eye margin. Terminal disks of fingers and toes slightly expanded. Mean tympanum/eye ratio slightly larger than 1/2. IMT rather large (ratio width/length less than 3/5). (2) *Dorsal color and pattern*: Uniformly yellow-orange or red-orange, without translucent shade, and with a black spot covering the tympanum and a little black pigment around the nostril. Bright red flashmarks present. Iris nearly uniformly black, only a little light pigment in its upper part. (3) *Ventral color and pattern*. Uniform, similar to dorsal surface but generally somewhat lighter. Area of “femoral glands” often speckled with blackish. Tibia bright red.

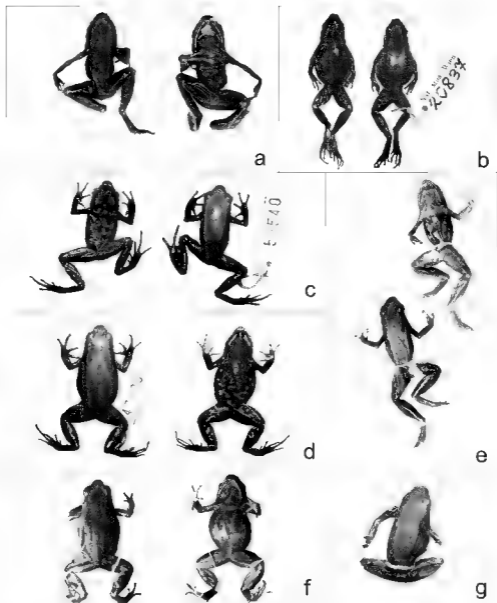


Fig 4 - Ventral and dorsal views of name-bearing types of *Mantella* species. (a) *M. betsileo* (lectotype, MNHN 1895.278), (b) *M. betsileo* (lectotype of *M. attenuata*, NMW 20817); (c) *M. expectata* (holotype, ZFMK 53540), (d) *M. viridis* (holotype, ZFMK 47900); (e) *M. luevigata* (holotype, TM 10074), (f) *M. madagascariensis* (holotype of *M. loppet*, NMB 4849), (g) *M. madagascariensis* (lectotype, MNHN 1895.276) Not to scale.

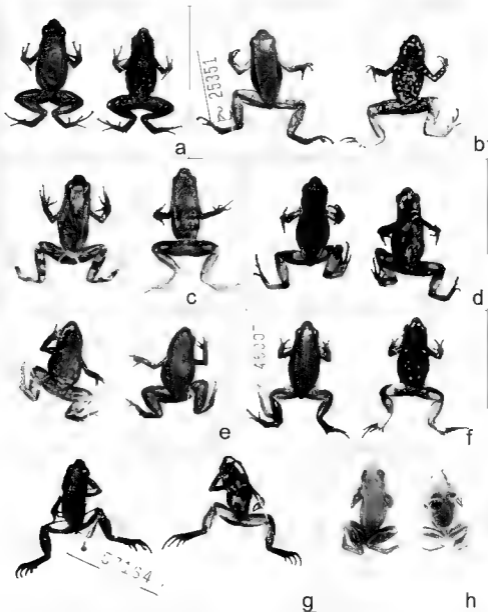


Fig. 5. Ventral and dorsal views of name-bearing types of *Mantella* species. (a) *M. nigricans* (lectotype, MNHN 1973 555), (b) *M. haraldmeieri* (holotype, ZFMK 25351), (c) *M. baroni* (holotype, BMNH 1947 2 7 19), (d) *M. covani* (lectotype, BMNH 1947 2 7 4), (e) *M. pulchra* (holotype, BMNH 1947 2 7 20), (f) *M. crocea* (holotype, ZFMK 45007), (g) *M. bernhardi* (holotype, ZFMK 57164), (h) *M. aurantiaca* (lectotype, MNHN 1899.412). Not to scale.

Mantella betsileo



ZFMK 17604



ZFMK 17605



GLAW & VENCES
(1994, fig 319)



ZFMK 62688



ZFMK 62696

***Mantella* sp. 1**



MNHN 1973 496



MNHN 1973 494



MNHN 1973 489



MNHN 1973 487



MNHN 1973 491

Mantella expectata



ZFMK 53541



ZFMK 53540



ZFMK 59096

Mantella manery



Holotype

Mantella viridis



ZFMK 47900



ZFMK 48046



ZFMK 48047



GLAW & VENCES
(1994, fig 318)

Fig. 6 - Variation of ventral pattern in species of the *Mantella betsileo* group



Fig 7 Variation of ventral pattern in *Mantella laevigata* and some species of the *M. cowani* group. Diagonally hatched areas represent light coloration which is different from the normal bluish or greyish (exceptionally greenish yellow) spots and markings on the black venter. A further differentiation of the light color was not undertaken, partly because in many preserved specimens the color is largely faded. The diagonally hatched areas thus comprise orange yellowish and light brown areas as well as the flashmark areas of some species which in life are vivid red.

Mantella baroni



MNHN 1933 247

MNHN 1991 1805

MNHN 1936.41

MNHN 1972 775

ZFMK 28870

Mantella cowani



MNHN 1973 528

MNHN 8594

MNHN 1973 529

Mantella crocea



ZFMK 52746

ZFMK 62764

ZFMK 62761

Mantella pulchra



ZFMK 62258

ZFMK 52122

GLAW & VENCES
(1994 fig. 330)

Mantella bernhardi



GLAW & VENCES
(1994 fig. 324)

ZFMK 62702

ZFMK 62705

Mantella madagascariensis



ZFMK 56154

ZFMK 14327

ZFMK 14326



ZFMK 56153



GLAW & VENCES
(1994 fig. 331)

Fig 8. Variation of ventral pattern in some species of the *Mantella cowani* group, and in species of the *M. madagascariensis* group, *M. bernhardi* group and *M. aurantiaca* group. See also legend of fig. 7

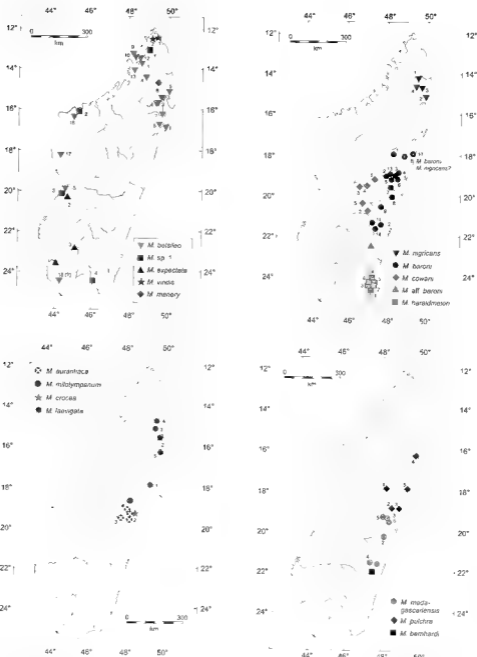


Fig 9 Distribution maps of *Mantella* species as distinguished in the present paper. Positioning of localities in the maps is only approximate and mainly based on BLOMMERS-SCHLOSSER & BLANC (1991)

KEY TO THE CURRENTLY KNOWN SPECIES OF *Mantella*

The following key should allow identification of all currently known *Mantella* species by their live coloration. Examination of both dorsal and ventral patterns is necessary for a reliable identification. Where useful, we also give morphological, ecological or bioacoustic characters as additional identification aids. A reliable identification of preserved specimens is not always possible, especially in formalin fixed individuals with faded pattern contrast, and in hybrid or rare intermediately colored specimens.

1. Ventral surface of hindlimbs partly or completely orange, yellow and/or red 2
 - Ventral surface of hindlimbs black with blue, whitish-blue or greyish markings, without orange or red elements 12
2. Dorsal coloration uniformly green, yellow, orange or reddish, with only rudimentary, dispersed black elements 3
 - Dorsally with distinct black or dark brown elements, often covering the largest part of dorsum and/or flanks 6
3. Ventral surface generally black with light markings, at least with some distinct black patterns 4
 - Ventral surface uniformly yellow or orange 5
4. Flank blotch area more densely covered by green/yellow than remaining flanks; flashmarks present *M. madagascariensis*, variable morph
 - Flank blotch area not more densely covered by green/yellow than remaining flanks; horseshoe marking and flashmarks present *M. crocea*
 - Flank blotch area more or less densely covered by green/yellow than remaining flanks; horseshoe marking and flashmarks absent *M. aff. baroni* (Andringitra)
5. Black pigment absent, skin often with a translucent shade *M. aurantiaca*
 - Black pigment present on tympanum and around nostril; skin without translucent shade *M. milotympanum*
6. Frenal stripe present 7
 - Frenal stripe absent 8
7. Flank blotches present, often integrated in an irregular network pattern of green/yellow and black *M. madagascariensis*, variable morph
 - Flank blotches absent, flanks anteriorly black, posteriorly of same color as dorsum *M. crocea*
8. Horseshoe marking present; chirp or trill calls 9
 - Horseshoe marking absent; single click calls 11
9. Small species (adult SVL 18-22 mm), IMT small, flank blotches very small, flanks thus nearly uniformly black; dorsum grey, with sharp but little distinct dorsolateral color border *M. bernhardi*

- Larger species (adult SVL 20-27 mm); IMT large; flanks black with large yellow, greenish or blue flank blotches 10
10. Dorsum, and especially dorsal head surface, brown, with a distinct dorsolateral color border to the black flanks; femur ventrally generally without red/orange color *M. pulchra*
Dorsum and head surface black (sometimes with green/yellow); femur ventrally generally with red/orange patterns *M. madagascariensis*
11. Dorsolateral color border present; flank blotches small, beige; hindlimbs dorsally brown *M. haraldmeieri*
Dorsolateral color border absent; flank blotches medium-sized, generally red; hindlimbs dorsally black with red *M. cowani*
Dorsolateral color border absent; flank blotches large and yellow or greenish; tibia, tarsus and foot dorsally orange with black *M. baroni* and *M. aff. baroni*
12. Frenal stripe and horseshoe marking absent 13
Frenal stripe present; horseshoe marking generally present *M. betsileo* group, 14
- 13 Throat generally uniformly black, without or with very few light markings; flank blotches absent; fingers and toes with largely expanded terminal disks; double click calls, partly arboreal habits *M. laevigata*
Throat black with light markings; flank blotches present, fingers and toes with moderately expanded terminal disks; single click calls, terrestrial habits *M. nigricans*
14. Flanks anteriorly black, posteriorly greenish, no dark crossband on tibia... *M. viridis*
Flanks anteriorly black, posteriorly brownish-red *M. sp. 1*
Flanks generally uniformly black or dark brown 15
15. Dorsum brownish; dark crossband on tibia present... .. *M. betsileo*
Dorsum yellowish, limbs blue to grey, dark crossband on tibia absent... .. *M. expectata*
Dorsum yellowish; limbs brown *M. manery*

DISCUSSION

RELIABILITY OF PUBLISHED DATA AND TREATMENT OF "PHANTOM NAMES"

During our survey of literature for the present paper, we became aware of many errors, especially regarding locality data. Furthermore, we noted that during the last years, hobbyists increasingly published unreliable or fantasy data on distribution, behaviour, variation and reproduction of *Mantella* species. With this statement, we do not want to downgrade publications of amateur herpetologists to *Mantella* knowledge in general. Several important contributions were published e.g. by ZIMMERMANN (1992, 1996a-b), MIER (1975, 1980, 1986) and STANISZEWSKI (1998b), among others. However, distributional data such as those of UNFRIED (1987), data on reproduction such as those of LE BERRÉ (1993; *M. laevigata* tadpoles

Table 3. – Phantom names of *Mantella* forms, their identity and current status. Additionally, the following phantom names (with clear mention of their conditional status) were listed by STANISZEWSKI (1998a): *Mantella spezei*, *Mantella crocea calxis*, *Mantella verronique*, *Mantella tulai*, *Mantella mangabe*.

Name	History of name	Taxonomic status	Nomenclatural status
<i>Mantella</i> "mysteriosa" BARTLETT, 1995	not used any more	<i>M. madagascariensis</i> , "variable morph"	conditional name (not available)
<i>Mantella nasuta</i> sp. CLARK, 1994	not used any more	<i>M. madagascariensis</i> , "variable morph"	nomen nudum (not available)
<i>Mantella aurantiaca rubra</i> Staniszewski, 1996	name used in several other hobbyist publications	synonym of <i>Mantella</i> <i>aurantiaca</i>	available name
<i>Mantella aurantiaca</i> <i>milotypanum</i> Staniszewski, 1996	name used in several other hobbyist publications	<i>Mantella</i> <i>milotypanum</i>	available name
" <i>Mantella marojezyi</i> ": STANISZEWSKI, 1996	name used in several other hobbyist publications	<i>Mantella manery</i> , described herein	conditional name (not available)
<i>Mantella</i> "marojezy" LARSEN, 1997	name used in several other hobbyist publications	<i>Mantella manery</i> , described herein	conditional name (not available)
<i>Mantella "negrinata"</i> LARSEN, 1997	name not yet used again	<i>Mantella nigricans</i>	conditional name (not available)

developing within two weeks), habitat data such as those of STANISZEWSKI in his 1997b booklet (e.g. *Mantella crocea* and *M. cowani* occurring in lowland forests), and lists of assumed new species as given in CLARK (1994), lack of any reliable data basis and must largely be seen as inventions of the authors or their informants. Especially the work of Andrew CLARK (1994) must be read with extreme caution in this respect. So, the information of a single specimen collected at high altitude on the Marojezy mountains which belongs to a new species and possibly new genus, quoted by CLARK (1994: 12) as personal communication of R. NUSSBAUM, is false; in fact, no such species was collected, and no such information provided to A. CLARK (NUSSBAUM, in litteris 1997). The major problem is that new scientific names are constantly coined in these papers. New *Mantella* names used without proper description and type designation for the taxon are here referred to as "phantom" names.

As discussed in the corresponding sections and summarized in tab. 3, most phantom names used until now are nomenclaturally not available since they must be regarded as nomina nuda due to the lack of a diagnosis, or as conditional names due to the use of quotation marks. Unfortunately, this does not apply to two of the names coined by STANISZEWSKI (1996), *M. aurantiaca rubra* and *M. milotypanum*, which are stabilized by lectotype designations in the present paper.

As a conclusion, editors of hobbyist journals should not permit their authors usage of new scientific names to name undescribed or undetermined morphs unless the names are accompanied by a formal description and type specimens are deposited in a publicly available scientific collection. Instead of phantom names, authors should be advised to refer to unknown morphs with numbers, letters or localities in quotation marks (e.g. *Mantella* sp. A., *Mantella* sp. 1, *Mantella* sp. "Marojezy").

According to the official information available in December 1998 on the ICZN webpage (www.iczn.org), the fourth edition of the *Code* will include the following requirements for new specific names proposed after 1999 to become available (slightly shortened in the following): (1) the new name must be explicitly indicated as being new (preferably by a term such as "sp. nov."); (2) the description will have to include the explicit fixation for it of a name-bearing type (a holotype or a syntype series); (3) when the name-bearing type of a species-group taxon proposed after 1999 consists of a preserved specimen or specimens, the proposal will be required to include a statement naming the collection(s) in which the name-bearing type is to be found.

Based on our experiences with *Mantella* phantom names, we strongly support these new requirements (as compared to the third *Code* edition currently in force) to valid species descriptions, which will at least avoid "accidental" taxa descriptions in hobbyist journals and pet dealer lists in the near future.

SPECIFIC STATUS

It must be stressed that the taxonomic status of several of the species as defined in the present paper is not yet totally clarified. This concerns *M. maneryi*, for which basic data on morphology and variation are lacking, the species of the *M. aurantiaca* group which appear to be very similar genetically (VENCES et al., 1999b), and *M. pulchra* which may be a subspecies of *M. madagascariensis*. It also concerns *M. aff. baroni*, R. NUSSBAUM (personal communication) collected specimens referable to this form at a locality south of Andringitra, confirming that it occupies a range between those of *M. baroni* and *M. haraldmeieri*. The specific status of these and the remaining taxa of the *M. cowani* group (all apparently distributed allopatrically) must still be confirmed. Specimens with intermediate color patterns are known which possibly are hybrids of *M. baroni* and *M. cowani* (personal observation), and others which may represent intermediates between *M. baroni* and *M. nigricans* (specimens from Zahamena and Fohohy; see section on *M. baroni*).

Generally, more detailed data of the species' distribution, variability and genetic differentiation in contact (hybrid?) zones are necessary. Some available data, however, already indicate a substantial amount of differentiation between the taxa mentioned above, so that attribution of specific status to them seems currently the most consistent hypothesis. Our proposal to consider all these forms as distinct species is based (1) on several biological indications, and (2) on practical reasons.

(1) Arguments for the specific distinctness between *M. haraldmeieri*, *M. cowani* and *M. baroni* are (a) the chromosomal differences between *M. baroni* and *M. haraldmeieri* (PINTAK et al., 1998), (b) the morphological differentiation of *M. cowani* (personal observation), and (c)

a relevant genetic differentiation between *M. baroni* and *M. cowani* (VENCES et al., 1999b). The specific status of the closely related, probably allopatric forms *M. madagascariensis* and *M. pulchra* is currently only corroborated by color differences and by a certain genetic differentiation detected by allozyme electrophoresis (VENCES et al., 1999b), but it cannot be excluded that *M. pulchra* is in fact a northern subspecies of *M. madagascariensis*. The very low genetic differentiation between all three species of the *M. aurantiaca* group (VENCES et al., 1999b; determined by allozyme electrophoresis) as well as the rather large color variability of *M. crocea* would support their status as color morphs of one single species. However, (a) the status of *crocea* as separate species was corroborated by chromosomal differences to *aurantiaca* (PINTAK et al., 1998), (b) relevant chromosomal differences were also found between *M. aurantiaca* and *M. milotympanum* (G. ODIERNA, personal communication), and (c) hybridizations in captivity between *M. aurantiaca* and *M. milotympanum* resulted in less vital offspring than simultaneously reared young of *M. aurantiaca* (personal observation).

(2) *Mantella* species are attractive animals which are often kept in captivity and traded in rather large numbers (BEHRA, 1993; GORZULA, 1996). To get an overview of the extent of trade and possibly necessary protection efforts and trade restrictions, it is often useful to have scientific names which can easily and reliably be assigned to forms with a certain, characteristic coloration. For example, *M. aurantiaca* as presently defined has been in the center of conservation efforts and discussions on trade restrictions (e.g. ZIMMERMANN, 1996a), and the inclusion of *M. crocea* and *M. milotympanum* as junior synonyms (respectively their posterior resurrection, since detailed future studies will possibly corroborate their specific distinctness) would cause confusion in conservation organizations and administrations, as for example in CITES authorities. These practical considerations are an additional support for our decision to assign species status to all currently distinguishable *Mantella* forms.

COLOR VARIABILITY

Our results allow for a first time to draw definitive statements on intrapopulational color variability in *Mantella* species. Earlier analyses (e.g. GUIBE, 1964: fig. 2-6) are confusing in this respect since they mixed several populations, belonging to different species, to demonstrate a presumed large variability in single taxa. In the following, we first summarize the current knowledge about intrapopulational color variability, and subsequently the known variability among different populations of the same species. Finally, we discuss deviating color morphs without reliably known localities.

Color and pattern variability within populations

(1) According to our data, dorsal and ventral coloration is rather uniform within populations of *M. baroni*, *M. betsileo*, and also in the one population of *M. aurantiaca* which we observed in the area of the Torotorofotsy swamps. (2) A slight variability is known in *M. laevigata* (Nosy Mangabe population), mainly regarding the posterior extension of the yellow-greenish dorsal color (GLAW & VENCES, 1992b). In *M. huradlmeieri*, the extension of flank blotches can vary between individuals (fig. 10). (3) An important variability is observed in the dorsal pattern (extension of yellowish/green color) of *M. nigricans* (Marojezy



Fig. 10. Size variation of flank blotches in *Mantella haraldmeieri* from the Chaînes Anosyennes. The dorsolateral color border is not sufficiently recognizable in the figured specimens and is therefore not included in the drawings.

population; see fig. 1g-h). In *M* sp. 1 from Ankarana, the extension of the fiery red flank color is very variable (VENCLES et al., 1996). Even more extreme variability is found in the dorsal pattern of *M*. aff. *baroni* as it is corroborated by MNHN vouchers which reliably were collected at the same locality. - (4) Too little is known for reliable statements on intrapopulation variation of the remaining species

Color and pattern variability among populations

(1) According to the existing data, differences are rather low between populations of *M* *baroni* (see also DALY et al., 1996 and ANDREONE, 1993), except for the deviating specimens from the localities Folohy and Zahamena at the probable northern distribution edge. Similarly, no differences are known between *M* *laevigata* populations. (2) Slight differences are known in *M*. *betsileo*, the Kirindy population differs from the east coast and Sambirano populations by reddish brown crossbands on the hindlegs, and a lighter leg color (VENCLES et al., 1996). - (3) Too few data are available on most other species; a high variability among populations may be found in the *M* *aurantiaca* group when more extensive fieldwork is carried out on these species. The same is true for *M*. *madagascariensis* (see below), in which the observed high variability may also be due to intrapopulation variation

Color and pattern variability in specimens without reliable locality information

(1) In some cases, deviating colorations have been observed in single specimens. One *M* *laevigata* specimen from the pet trade had brown instead of black legs (GLAW et al., 1998).



M. madagascariensis lectotype
MNHN 1895.276



M. madagascariensis
MNHN 1935.416 (paratype *loppei*)



M. madagascariensis
ZFMK 62741 (left)
ZFMK 62740 (right)



M. baroni
MNHN 1991.1805



M. aff. baroni
MNHN 1991.1804



M. haraldmeieri
MNHN 1973.508



M. cowani
MNHN 1973.528

Fig. 11 Pattern on posterodorsal femur and knee hollow in the lectotype of *Mantella madagascariensis* and in several *Mantella* species which occur in the Eastern, Central and South-Eastern Regions of Madagascar. The pattern of the lectotype clearly corresponds best to that of the paratype of *M. loppei* (to be considered as junior synonym of *M. madagascariensis*) and to other specimens here considered as *M. madagascariensis*. The dotted line on the femur of the ZFMK specimens marks the (sharp) color border between yellow (above) and orange (below) which is only visible in life or shortly after preservation. Regarding dorsolateral color border of *M. haraldmeieri*, see caption of fig. 10.



M. madagascariensis lectotype
MNHN 1895 276



M. madagascariensis
MNHN 1935 416



M. baroni
MNHN 1991.1805



M. aff. baroni
MNHN 1991 1804



M. cowani
MNHN 1973 528



M. haraldmeieri
MNHN 1973 508



M. bernhardi
ZFMK 57164 (holotype)

Fig 12 Ventral pattern on femur and tibia in the lectotype of *Mantella madagascariensis* and in several *Mantella* species which occur in the Eastern, Central and South-Eastern Regions of Madagascar. The pattern of the lectotype clearly corresponds best to that of the paratype of *M. loppet* (MNHN 1935 4.6), but not to *M. bernhardi* which has a ventrally uniformly light femur

(2) Specimens with intermediate coloration (possibly in some cases due to hybridization) are known between *M. baroni* and *M. cowani* (personal observation), and between *M. nigricans* and *M. baroni* (specimens from Folohy and Zahamena). Also, *M. crocea* specimens are known which have a nearly uniform (greenish or yellowish) dorsal color, with only remains of a dark ventral pattern, and thus appear very similar to *M. milotympanum* (GLAW & VENCES, 1998).

(3) DALY et al. (1996) were right in stating that information based on specimens from the pet trade should be seen with caution, but large series of specimens seen in the cages of the same dealer at the same time (personal observation) allow, in our opinion, the conclusion of important variability (dorsally and ventrally) in *M. madagascariensis*. Whether this variability is between different uniform populations, or within single variable populations, cannot be decided at the current state.

Causes of variation

As in dendrobatids (MYERS & DALY, 1983), the evolutionary mechanisms causing the observed intrapopulation variation (contrasting with the uniformity in other populations) in some species are not yet understood. Considering the presence of skin alkaloids in *Mantella* (DALY et al., 1996), their coloration can be seen as largely aposematic. It is thus possibly subject to strong predatory selective pressures, and phenomena of Müllerian mimicry, which seem to be exceptional among anurans (DUELLMAN & TRUEB, 1985), may also be involved

SYNTOPY

According to the data presented herein, the following reliable cases of syntopic occurrence of different *Mantella* species are known (the possible syntopic occurrence of *M. expectata*, *M. betsileo* and *M. sp. 1* near Morondava needs confirmation): (1) *M. baroni*/*M. pulchra* (An'Ala; ANDREONE, 1993, DALY et al., 1996; personal observation), (2) *M. baroni*/*M. madagascariensis* (Vohiparara, personal observation, Niagarakely, based on ZFMK vouchers); (3) *M. nigricans*/*M. laevigata* (Marojezy, Camp 3, personal observation); (4) *M. laevigata*/*M. manery* (Marojezy, Camp 1; personal observation); (5) *M. laevigata*/*M. betsileo* (Mananara, DALY et al., 1996); (6) *M. betsileo*/*M. pulchra* (Mananara, DALY et al., 1996)

It is remarkable that these few cases all refer to species of different species groups occurring syntopically. On the other hand, in several groups the species appear to be allopatrically distributed. This is most distinct in the *M. cowani* group (see fig. 9). Also the two taxa of the *M. madagascariensis* group seem to be distributed in an allopatric north-south pattern, whereas the species of the *M. aurantiaca* group are probably distributed parapatrically in swamp forest and rain forest areas in the east. Only in the *M. betsileo* group are the areas of different forms (*M. betsileo*, *M. sp. 1*, *M. expectata*) known to overlap. It is not known whether in these overlap areas the distribution patterns are at least locally of close syntopy or always of parapatry.

Table 4. – Regional endemism in *Mantella* species.

Region	Number of species	Number of endemic species	Endemism
South-West	2-3	0	0 %
West	2-3	0	0 %
South-East	1	1	100 %
East	10	8	80 %
Center	1	1	100 %
North-East	4	2	50 %
Northern Center	1	0	0 %
North	2	1	50 %
Sambirano (N.-W.)	1	0	0 %

BIOGEOGRAPHY

The almost complete re-examination of the historical voucher specimens and review of recent field data in the present paper enabled us to present updated distribution maps. The resulting distribution patterns of many species, especially those of the *M. cowani* group, are very different from those presented by BUSSE (1981) and BLOMMERS-SCHLÖSSER & BLANC (1991).

All *Mantella* species are exclusively distributed on Madagascar and its adjacent islets (Nosy Be, Nosy Komba, Nosy Boraha, Nosy Mangabe). Records of *Mantella* species on La Réunion island (THOMINOT, 1889; GUIBÉ, 1964) or the Seychelles (STANISZEWSKI, 1997b) are not corroborated by reliable voucher specimens, and must be considered as wrong.

Most *Mantella* species inhabit areas of tropical rainforest but at least three species (*M. expectata*, *M. betsileo*, *M. sp. 1*) are known from arid regions in western Madagascar. Although there are no reliable altitude data for most localities, it can be stated that they are mostly in-between sea level and ca. 1000 m altitude. Only *M. cowani* is known to occur at much higher altitudes (Ambatodradama: 2000 m).

According to ANGEL (1942), as modified by BRYGOO (1971), GLAW & VENCES (1994) and RAXWORTHY & NUSSBAUM (1995), Madagascar was herpetogeographically divided into the Eastern Domain and the Western Domain, each consisting of various regions. The Western Domain contains the Western and South-Western Regions, the Eastern Domain contains the South-Eastern, Eastern, Southern Central, Central, North-Eastern, Northern Central, Northern and Sambirano (North-Western) Regions. Here we follow the delimitation of regions in the map 3 of GLAW & VENCES (1994).

In contrast to other terrestrial vertebrate groups as the dwarf chameleons of the genus *Brookesia* (see RAXWORTHY & NUSSBAUM, 1995), the northern biogeographic regions (North-West, North, Northern Center, North-East) do not appear to be a diversity center for *Mantella* (as compared to the Eastern Region, see tab. 4). All six species groups defined herein have representatives in the Eastern Region, whereas only three (*M. laevigata* group, *M. betsileo* group, *M. cowani* group) have representatives in one of the northern regions. The Eastern Region harbours at least 10 *Mantella* species, whereas only between one and four species are known from each of the northern regions (six species altogether). None of the species groups is endemic to the northern regions, whereas three species groups are endemic to the East. Three species (*M. viridis*, *M. manery*, *M. nigricans*) are endemic to the northern regions, whereas eight species are endemic to the East.

However, these counts may draw a biased picture since many species of the East show in fact a very low genetic differentiation (VENCES et al., 1999b), and some species complexes may better be seen as single units for biogeographic comparisons. Counting the *M. aurantiaca* group and the *M. madagascariensis* group as single units, and seeing *M. aff. baroni* as closely related to *M. baroni*, reduces the importance of the Eastern Region as center of diversity and, especially, endemism of *Mantella*. It also is interesting that the northern regions are mainly inhabited by species which are considered as relatively basal within the genus (PINTAK et al., 1998; VENCES et al., 1999a-b). *M. laevigata* and the *M. betsileo* group. Also *M. nigricans*, due to the lack of reddish ventral hindleg color, can be seen as the most basal representative of the *M. cowani* group.

CONSERVATION

Among the anurans of Madagascar, and beside the tomato frogs (*Dyscophus antongili* and *D. guineti*), *Mantella* is certainly the group most attractive to the pet trade. According to BEHRA (1993), a total of 10597 *Mantella* specimens were legally exported from Madagascar in the first half of 1990. *Mantella* species have been subject of discussions on trade restrictions and CITES inclusion. During several years, *Mantella aurantiaca* was the only species included in the CITES regulation (appendix 2) due to its assumed restricted distribution and vulnerability. In 1997, inclusion of several other species (*M. haraldmeieri*, *M. bernhardi*, *M. cowani* and *M. viridis*) was discussed. Also, *Mantella* have been used as key species for the justification of expansion or implementation of natural reserves (e.g. ZIMMERMANN, 1996).

The basis of all these discussions were the published distributional data and species definitions, as well as some unpublished reports. For statements on vulnerability by excessive collecting or habitat destruction, and identification of conservation priorities, a comparative assessment of the status of all *Mantella* species is necessary. In the following we analyze five different factors which may influence the status of *Mantella* species.

(1) *Geographical distribution of the species* – We estimated the extent of the distribution area and the density by which it is populated by a certain species by the total number of localities known and the largest distance in kilometers between two locality records attributed to the species. Species can be classified as follows (a) common species with a large distribution

area (≥ 10 localities, and > 400 km distance between the most distant localities): *M. betsileo*, *M. baroni*, (b) more localized species with a large distribution area (≤ 5 localities, > 400 km distance): *M. sp. 1*, (c) relatively common species with a moderate distribution area (> 5 localities, 100-400 km distance): *M. laevigata*, *M. madagascariensis*, *M. cowani*, (d) more localized species with a moderate distribution area (< 5 localities, 100-400 km distance): *M. expectata*, *M. pulchra*, (e) species with a small distribution area (≥ 3 localities, 50-100 km distance): *M. nigricans*, *M. haraldmeieri*, *M. aurantiaca*; (f) localized species which are only known from one or two localities (distance < 50 km): *M. manery*, *M. viridis*, *M. bernhardi*, *M. crocea*, *M. milotympanum*.

(2) *Number of nature reserves and protected areas in which a species is known to occur* At present, this is known to apply to the following species and localities: *M. betsileo*, Tsaratanana, Mananara, Masoala, Lokobe, Manongarivo, Tsingy de Bemaraha, *M. sp. 1*, Ankarana; *M. expectata*, Isalo; *M. manery*, Marojezy; *M. laevigata*, Mananara, Nosy Mangabe, Anjanaharibe-Sud, Marojezy, *M. baroni*, Analamazoatra, Mantady, Ranomafana, probably Zahamena; *M. aff. baroni*, Ivohibe; *M. nigricans*, Anjanaharibe-Sud, Marojezy, probably Masoala, *M. haraldmeieri*, possibly Andohahela; *M. madagascariensis*, Ranomafana; *M. pulchra*, Mananara, *M. aurantiaca*, not yet known from any protected area (would occur within the limits of Analamazoatra if this reserve was expanded as suggested by ZIMMERMANN, 1996b).

(3) *Restriction of the species to primary (forest) habitat.* - Field data are lacking or insufficient for most *Mantella* voucher specimens examined in the present study. However, some authors give reliable habitat data of *Mantella* species, which are here combined with our personal observations. Species which are until now only found in primary rainforest are *Mantella laevigata* (localities Nosy Mangabe, Marojezy, personal observation, Anjanaharibe, Tsararano: personal communication of F. ANDREONE), *M. baroni* (several localities; ANDREONE, 1993, DALY et al., 1996, personal observation), *M. haraldmeieri* (pristine and degraded primary forest near Nahampoana, personal observation), *M. nigricans* (Marojezy, Tsararano, Anjanaharibe, personal communication of F. ANDREONE and personal observation), *M. manery* (personal observation), *M. madagascariensis* (Ranomafana; personal observation), *M. pulchra* (several localities, ANDREONE, 1993, DALY et al., 1996, personal observation), *M. aurantiaca* (swamp forest near Andasibe; personal observation, ZIMMERMANN et al., 1990), *M. crocea* (swamp forest; DALY et al., 1996), and *M. bernhardi* (a single specimen found in degraded primary forest rests near rice fields; personal communication of F. ANDREONE). Species known from more arid forest are *M. viridis* (personal observation at Montagne des Français, see also DALY et al., 1996), *M. expectata* (Isalo, DALY et al., 1996) and *M. sp. 1* (Ankarana; personal communication of J. KÖHLER). Only *M. betsileo* is known to occur regularly outside primary habitats (personal observation on Nosy Be, Nosy Komba, Nosy Boraha and near Maroantsetra). For the remaining species, no reliable field observations are available to us, however, it is to be expected that *M. milotympanum* is restricted, as *M. aurantiaca*, to swamp forests.

(4) *Extent of trade of the species* Although trade statistics do exist, a comparison of numbers of traded specimens between species is not possible due to taxonomic confusion in the past. In many cases, it is not possible to state which species actually was traded under a certain name. Therefore we prefer to summarize our subjective impressions made between

Table 5. - Conservation status and trade of *Mantella* species. For each species we give the number of known localities, the maximum distance between the most distant known localities (± 20 km) measured on a 1:2,000,000 map (*Carte routière, Foiben Taosarintann'i Madagasikara* [Institut National de Géodésie et Cartographie, Madagascar]) as very rough estimate of the distribution area; the number of nature reserves in which the species is known to occur; its known restriction to primary forest habitat (+ restricted to primary forest; - not restricted to primary forest); the frequency in which we have seen it in trade (only our subjective impressions between 1990-1997: - not exported in relevant numbers, + exported, ++ often exported); and the potential attractiveness for hobbyists and the pet trade (+ not very attractive, ++ attractive, +++ very attractive) Status is coded as follows: OK, not threatened, CT, commercially threatened (potential danger of overcollecting exists at least locally); R, rare; K, insufficiently known, I, indeterminate; V, vulnerable. Research needs are coded as follows 1, distribution; 2, taxonomic status and validity; 3, variation, 4, habitat

<i>Mantella</i> species	Number of localities	Maximum locality distance	Number of reserves	Restriction to primary forest	Traded	Attractiveness	Status	Research needs
<i>M. betsileo</i>	17 (18)	840 (1220) km	6	-	+	+	OK	-
<i>M. sp. 1</i>	5	1260 km	1	(-)		+	K	2, 3
<i>M. viridis</i>	2	< 20 km	0	(-)	++	++	R	1
<i>M. expectata</i>	3	340 km	1	(-)	+	+++	R	1, 4
<i>M. manery</i>	1	0 km	1	+	-	++	K	1, 2, 3, 4
<i>M. laevigata</i>	5	360 km	4	+	+	+++	CT	-
<i>M. nigricans</i>	4	80 km	3	+	-	++	CT	2
<i>M. haraldmeieri</i>	6	50 km	1?	+	-	+	R	2
<i>M. baroni</i>	16 (18)	420 km	3 (4)	+	++	+++	CT	-
<i>M. aff. baroni</i>	1	0 km	1	?	-	+++	K	1, 2, 3, 4
<i>M. cowani</i>	5	160 km	0	?	++	+++	R	1, 2, 3, 4
<i>M. bernhardi</i>	1	0 km	0	+?	+	+	V	1, 4
<i>M. pulchra</i>	5	320 km	1	+	+	++	CT	2, 3
<i>M. madagascariensis</i>	5	260 km	1	+	++	+++	CT	3, 4
<i>M. crocea</i>	1?	0 km	0	+?	+	++	I	1, 2, 3, 4
<i>M. aurantiaca</i>	4	60 km	0	+	++	+++	V	1, 3
<i>M. milotympanum</i>	1	0 km	0	?	+	+++	I	1, 2, 3, 4

1990 and 1997. In these years, we monitored several times the exhibitions of specialized pet dealers in Germany as well as in Madagascar, and thus got some indications on extent of trade of certain species which are summarized in tab. 5. Our impressions are relatively well in accordance with the data of GORZULA (1996), who reported the incidence of *Mantella* species among a sample of 69 European hobbyists: *M. aurantiaca*, 15.9%; *M. madagascariensis* (probably partly referring to *M. baroni*) and *M. crocea*, 14.5% each, *M. cowani* (possibly also largely referring to *M. baroni* or *M. madagascariensis*), 11.6%; *M. pulchra*, 4.4%; *M. viridis*, 2.9%; *M. betsileo* and *M. haraldmeieri*, 1.5%. Also the list of BEHRA (1993) of *Mantella* exported in 1990 from Madagascar does not contradict our observations. *M. aurantiaca*,

30.5 %; *M. viridis*, 14 %; *M. betsileo*, 3 %; *M. cowani* (probably largely referring to *M. baroni*), 29 %, undetermined species, 23 %.

(5) *Potential subjective attractiveness to hobbyists*, estimated by amount of colorful pattern and interest of breeding biology (in *M. laevigata*).

To summarize these data, we tried to assign status categories to *Mantella* species. We followed categories used in the European CITES regulations (ANONYMOUS, 1996), except the category CT ("commercially threatened") which we used in a modified way as specified below, and the abbreviation OK which we used for non-threatened species.

(1) *OK (not threatened)* - Not threatened at present is *M. betsileo*, which has a low attractiveness, a very large distribution area, and also occurs outside primary forest.

(2) *K (insufficiently known)*. *M. manery* and *M. aff. baroni* are expected to belong to one of the categories below (probably R), but basic information is lacking. *M. sp. 1* does not seem to be threatened at the moment due to its low attractiveness and apparently large distribution area; this species, however, may be more locally restricted than *M. betsileo*, and more dependent on a threatened habitat type (dry forest). Also in this case, more data are needed

(3) *CT (commercially threatened)*. - This category is here used for species which may be locally and potentially affected by overcollecting due to their high attractiveness, but which are not yet threatened in their whole distribution area. In this category, we include *M. laevigata*, *M. nigricans*, *M. baroni*, *M. pulchra* and *M. madagascariensis*.

(4) *R (rare)* - Species with restricted distribution areas which are not yet vulnerable or endangered, but are at risk. In this category, we include *M. viridis*, *M. expectata* and *M. cowani*.

(5) *V (vulnerable)* - Species likely to become soon endangered by extinction if causal factors continue operating. At present, we only include *M. aurantiaca* and *M. bernhardi* in this category.

(6) *I (indeterminate)* - Species known to be endangered, vulnerable or rare, but for which there is not enough information to say which of the categories is appropriate. We include *M. crocea* and *M. milotympanum* in this category

We do not yet assign any known *Mantella* species to the "endangered" category (species facing a very high risk of extinction in the wild in the near future), but some species might move to this category within the next ten years.

Considering the lack of basic knowledge on distribution, variation, and taxonomic status of many *Mantella* species, and the vulnerability of several of them (see tab. 5), we propose the following research priorities:

(1) Clarification of taxonomy and distribution of the species of the *M. aurantiaca* group, by detailed mapping of color morph occurrence and genetic studies along hybrid zones. Single voucher specimens from each recorded locality should be deposited in publicly available scientific collections.

(2) Habitat descriptions and mapping of *M. expectata*, *M. cowani* and *M. bernhardi*

- (3) Clarification of the taxonomic status of *M. aff. baroni* and of *M. baroni* from the Zahamena area.
- (4) Studies on variability in the *M. madagascariensis* group (status of *M. pulchra*, identity of the "variable morph(s)" of *M. madagascariensis*).
- (5) Formal description and naming of *M. sp. 1*.
- (6) Comparative studies on the microhabitat and ecology of all *Mantella* species.

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Corresponding editor: Alain DUBOIS.

Une nouvelle espèce du genre *Leptodactylodon* (Arthroleptidae, Astylosterninae) du Gabon

Annemarie OHLER

Laboratoire des Reptiles et Amphibiens,
Muséum national d'Histoire naturelle,
25 rue Cuvier, 75005 Paris, France
E-mail: ohler@mnhn.fr

A new species of astylosternine frog is described from Lopé Fauna Reserve, Gabon. The new species is close to *Leptodactylodon albiventris* and is characterized by its relatively long vomerine ridges, its emarginate tongue, its brownish dorsal color with small white spots, and, in adult male, its metacarpal with three spines and its first finger with four spines; throat is black-violet, vent dark brown with white marbling and the underside of thigh is yellowish. This is the first record of the genus *Leptodactylodon* in Gabon; this genus is known therefore from Nigeria, Cameroon, Equatorial Guinea and Gabon.

INTRODUCTION

Le genre *Leptodactylodon* Andersson, 1903 (Arthroleptidae, Astylosterninae) inclut actuellement onze espèces et quatre sous-espèces. *L. albiventris albiventris* (Boulenger, 1905); *L. albiventris bueanus* Amiet, 1980; *L. axillaris* Amiet, 1971; *L. bicolor* Amiet, 1971; *L. boulengeri* Nieden, 1910; *L. erythrogaster* Amiet, 1970; *L. mertensi* Perret, 1959; *L. ovatus* Andersson, 1903; *L. perreti* Amiet, 1971; *L. polycanthus polycanthus* Amiet, 1970; *L. polycanthus orientalis* Amiet, 1971; *L. ventrumarmoratus* (Boulenger, 1904). Il n'est connu que du Cameroun, où AMIET (1980) a reconnu 11 espèces et 4 sous-espèces, de l'est du Nigeria, où se rencontre une seule de ces onze espèces, et de Guinée Equatoriale, où DE LA RIVA (1994) a signalé *L. albiventris*. AMIET (1980) a fait une révision du genre et a discuté les relations évolutives et biogéographiques au sein de celui-ci. Il a également proposé une interprétation de la position de *Leptodactylodon* parmi les Astylosterninae.

Leptodactylodon est donc maintenant un genre bien étudié pour lequel nous disposons d'une révision systématique de qualité. Quand nous avons observé, parmi d'autres recoltes faites par Charles P BLANC dans la Réserve de faune de la Lopé au Gabon, un spécimen mâle adulte du genre *Leptodactylodon*, la tâche de détermination nous a semblé aisée. Nous nous sommes ainsi très rapidement aperçue que cette petite grenouille ne peut être attribuée à aucune des formes reconnues par AMIET (1980). Nous sommes ainsi dans la situation embarrassante de devoir décrire une nouvelle espèce sur un spécimen unique, travail qui n'est

possible que par rapport au riche matériel étudié en détail par AMIET, et également parce que ce spécimen est un mâle adulte et montre plusieurs caractères importants en systématique du genre *Leptodactylodon*.

Leptodactylodon Andersson, 1903

Leptodactylodon Andersson, 1903 141 - Espèce-type: *Leptodactylodon ovatus* Andersson, 1903, par monotypie

Bulua Boulenger, 1904 262 Espèce-type: *Bulua ventrimarmorata* Boulenger, 1904, par monotypie.
Synonymie: ANDERSSON, 1905: 22.

Leptodactylodon blanci sp. nov

(fig. 1-3)

Holotype MNHN 1996.8876, mâle adulte, récolté par Charles P BLANC en mars 1995.

Localité-type. Campement SOFORGA (0°36'30"S, 11°31'59"E), Réserve de faune de la Lopé (voir BLANC, 1998), Gabon.

Diagnose. - Petite espèce de *Leptodactylodon*, mâle adulte de 22,1 mm; dents vomériennes en deux séries assez longues atteignant le bord extérieur des choanes; langue échancrée, métacarpien avec trois épines, doigt I avec 4 épines; coloration dorsale brun uni avec petits points blancs et une zone plus claire près du cloaque; gorge noir violacé avec taches blanches indistinctes, ventre brun foncé avec marbrures blanches nettes; dessous des cuisses jaune clair uni.

Description de l'holotype MNHN 1996.8876, mâle adulte de petite taille (longueur museau-anus 22,1 mm), corps ramassé (fig. 1). Tête plus large (10,0 mm) que longue (9,2 mm); museau arrondi, dépassant à peine le bord antérieur de la bouche, sa longueur (3,76 mm) plus longue que le diamètre de l'œil (2,72 mm); canthus rostralis arrondi, concave et région canthale faiblement inclinée. Espace interorbitaire plat, plus large (2,92 mm) que la largeur de la paupière (2,01 mm), mais bien moins large que la distance internasale (3,95 mm); narnes plus proches de l'œil (1,16 mm) que de l'extrémité du museau (2,14 mm). Pupille arrondie. Tympan présent, plutôt indistinct, son diamètre (1,00 mm) un tiers du diamètre de l'œil, aucun vestige d'ocelle pinéal. Crêtes vomériennes (fig. 2) présentes avec une dizaine de petites dents chacune, perpendiculaires à l'axe du corps, postérieures aux choanes, et touchant celles-ci, les rangées de dents bien plus longues que la distance les séparant. Langue de taille moyenne, en forme de cœur avec une petite échancrure. Repli supratympanique peu distinct, de l'œil à l'épaule.

Bras court, avant-bras (5,64 mm) plus long que la main (5,38 mm) (fig. 3b), doigts plutôt longs et plutôt larges; doigt I égal au II, le II plus court que le IV, le doigt III le plus long (3,05 mm), extrémités de tous les doigts pointues, non élargies, avec ventouses portant des sillons ventro-latéraux; sillons proximaux absents, bords dermiques le long des doigts I à III des 2 cotés, palmure absente; tubercules sous-articulaires distincts, arrondis, simples, tous présents; tubercules métacarpiaux ovales, bien développés; deux tubercules palmaires ovales, bien développés; tubercules surnuméraires à la base des doigts absents.



Fig 1. *Leptodactylodon blanci*, holotype MNHN 1996 8876, mâle adulte. A gauche, vue dorsale, à droite, vue ventrale.



Fig 2. *Leptodactylodon blanci*, holotype MNHN 1996 8876, mâle adulte. Crêtes vomériennes.

Jambe trois fois plus longue (10,2 mm) que large (3,5 mm), plus courte que la cuisse (10,7 mm), et que la distance entre la base du tubercule métatarsien interne et l'extrémité de l'orteil IV (11,5 mm) (fig 3a); longueur relative des orteils $I < II < V < III < IV$. Extrémités de tous les orteils pointues, faiblement élargies, portant des ventouses avec sillons ventrolatéraux, sillons proximaux absents. Palmure absente. Bord dermique sur l'orteil V absent. Tubercules sous-articulaires nets, ovales, tubercule métatarsien interne court, proéminent, sa longueur (2,20 mm) contenue 2,5 fois dans la longueur de l'orteil I (5,44 mm); tubercule métatarsien externe absent; tubercules surnuméraires absents; tubercules tarsiens absents, pli tarsien absent.

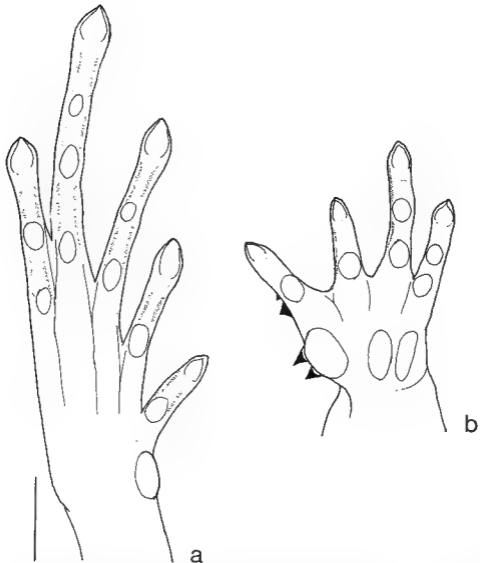


Fig. 3 - *Leptodaetylodon blanci*, holotype MNHN 1996 8876, mâle adulte (a) pied, vue ventrale; (b) main, vue ventrale

Dessus et côté de la tête ainsi que dos lisses; flancs avec pustules effacées; membres antérieurs lisses; membres postérieurs avec pustules peu nettes; face inférieure lisse, présence de spinules cornées au bord antérieur de la gorge.

Dos, dessus et côté de la tête, haut du flanc et avant-bras brun foncé avec petits points blancs, barre blanche reliant le tiers antérieur des yeux et quart postérieur du dos brun plus

clair, dessus de la cuisse et partie proximale de la jambe brun foncé avec petits points blancs, partie distale de la jambe et tarse beiges avec points bruns, séparée de la partie brun foncé par une large bande brun noirâtre; partie postérieure de la cuisse blanchâtre couverte de mouchetures brunes denses. Gorge noir violacé avec quelques taches blanches indistinctes; bord de la gorge brun avec taches blanches; poitrine et ventre brun avec vermiculations blanches nettes. Dessous des cuisses jaunâtre uniforme.

Caractères sexuels secondaires mâles. – Trois épines nuptiales sur le métacarpien et quatre sur le doigt I, de couleur noire; petites spinules transparentes sur le bord antérieur de la gorge; sac vocal externe unique, ouvertures arrondies de chaque coté en arrière dans la bouche.

Ecologie. – BLANC (1998) décrit le milieu d'origine de l'holotype comme suit: "forêt dense: sous-bois; ruisseau; camp abandonné; pistes". Sur le même site, 8 autres espèces d'Amphibiens ont été capturées: *Alexeteron* sp.; *Arthroleptis sylvaticus* (Laurent, 1954); *Bufo latifrons* Boulenger, 1900; *Conraua crassipes* (Buchholz & Peters, 1875); *Dimorphognathus africanus* (Hallowell, 1857), *Phrynobatrachus cornutus* (Boulenger, 1906); *Phrynobatrachus* sp.; *Ptychadena perreti* Guibé & Lamotte, 1958.

Etymologie – L'espèce est dédiée à Charles P. BLANC qui a récolté le spécimen et nous l'a confié pour description.

DISCUSSION

AMIET (1980) présente une clef de détermination du genre *Leptodactylodon* que nous avons reprise ici (Annexe 1), en insérant la nouvelle espèce, sur la suggestion d'un lecteur qui pensait qu'il serait souhaitable de la mettre à disposition d'un plus large public, la clef originale étant parue dans un journal absent dans de nombreuses bibliothèques.

Le genre *Leptodactylodon* peut être divisé en quatre groupes d'espèces: (1) un groupe (groupe de *L. mertensi*) qui comporte des espèces dont les mâles portent des protubérances axillaires et qui se caractérisent par l'atrophie des dents vomériennes (*L. mertensi*, *L. erythro-gaster*, *L. perreti*, *L. axillaris*); (2) un groupe (groupe de *L. bicolor*), comportant une seule espèce, caractérisée par l'atrophie des dents vomériennes et l'absence des protubérances axillaires; (3) un groupe (groupe de *L. ornatus*), comportant une seule espèce, montrant une langue non-échancrée et dont les mâles présentent une seule épine sur le métacarpe, et (4) un groupe (groupe *L. ovatus*) montrant plusieurs épines sur le métacarpe et une langue échancrée (*L. ovatus*, *L. boulengeri*, *L. ventrimarmoratus*, *L. albiventris*, *L. polycanthus*)

La nouvelle espèce se place dans ce dernier groupe. Dans sa clef, AMIET (1980) y a distingué deux sous-groupes par la taille des espèces et par la formation de leurs crêtes vomériennes. On ne peut pas assigner *L. blanci* facilement à l'un des deux sous-groupes. La nouvelle espèce est certes de petite taille, mais par l'extension de ses crêtes vomériennes elle semble intermédiaire. Sa livrée dorsale et sa taille ressemblent à celles de *L. bicolor*, mais elle se distingue de cette espèce par la présence de dents vomériennes et par l'absence de tout dessin sur les cuisses; les taches blanches sur le ventre sont plus denses et de taille inférieure

chez *L. blanci*. Cette livrée dorsale "bicolore" se rencontre également dans la sous-espèce *L. albiventris bueanus*. Morphologiquement, cette forme semble plus proche encore de la nouvelle espèce, notamment par la présence de dents vomériennes et son nombre d'épines métacarpiales de 3. Les deux formes se distinguent néanmoins par la coloration ventrale chez les deux sous-espèces d'*albiventris*, seule la gorge est foncée avec des taches plus claires.

Ce spécimen témoigne de la présence de *Leptodactylodon* au Gabon et amène à augmenter l'aire de distribution du genre vers le sud. Ainsi cette aire inclut actuellement le Nigéria, le Cameroun, la Guinée Equatoriale et le Gabon.

RÉSUMÉ

Une nouvelle grenouille de la sous-famille Astylosterninae est décrite de la Réserve de faune de la Lopé au Gabon. Cette nouvelle espèce se rapproche de *Leptodactylodon albiventris* et se caractérise par des crêtes vomériennes assez longues, sa langue échancrée, la présence de trois épines sur le métacarpe, la présence de quatre épines sur le premier doigt et le dos de couleur brune avec des petits points blancs; la gorge est violet noirâtre, le ventre brun foncé avec des marbrures blanches et le dessous des cuisses est jaunâtre. Ce spécimen représente la première mention du genre *Leptodactylodon* au Gabon, le genre est donc connu du Nigéria, du Cameroun, de la Guinée Equatoriale et du Gabon.

REMERCIEMENTS

Charles P. BLANC a collecté le spécimen et me l'a confié pour étude. Je remercie Alain DUBOIS pour ses remarques, comme toujours très qualifiées, sur le manuscrit.

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ANNEXE I

CLEF DE DÉTERMINATION DES ESPÈCES ET SOUS-ESPÈCES DE *LEPTODACTYLODON*

- 1 Dents vomériennes bien développées, disposées en bandelettes de forme variable 2
 - Dents vomériennes atrophiées, formant 2 petites saillies arrondies, ou absentes 12
- 2 Dents vomériennes disposées en accent circonflexe, langue non échancrée à son extrémité, une bande dorsale sub-rectangulaire foncée; côtés de la tête, dessous des pieds et marques para-anales foncées, 1 seule épine métacarpienne chez le mâle (groupe de *L. ornatus*) 3
 Dents vomériennes en bandelettes rectilignes ou arquées, langue échancrée, pattern dorsal et latéral peu marqué ou indistinct, plusieurs épines métacarpiennes chez le mâle (groupe de *L. ovatus*) 4
- 3 Face ventrale, membres postérieurs exceptés, vermiculée de blanc et noir *L. ornatus ornatus*
 - Face ventrale, y compris les membres postérieurs, noire avec de grosses taches blanches plus ou moins arrondies *L. ornatus permaculatus*
- 4 Taille grande (35 à 44 mm env); dents vomériennes en longues bandelettes dépassant les choanes vers l'extérieur et étroitement rapprochées, face ventrale, au moins la gorge, ponctuée ou marbrée de blanc et noir; 3, 4 ou 5 épines métacarpiennes chez le mâle 5
 Taille médiocre (au max 30 mm chez les femelles, en moyenne 25-26 mm chez les mâles), dents vomériennes en bandelettes courtes, écartées et ne dépassant pas ou à peine les choanes vers l'extérieur, livrée ventrale souvent uniforme ou brun avec vermiculations blanches, 2-3, 4 ou 5-6 épines métacarpiennes chez le mâle 8
- 5 Région inguinale marbrée ou largement maculée de sombre sur fond clair, ce pattern pouvant s'étendre à la face antérieure des cuisses (*L. ovatus*) 6
 - Région inguinale non marbrée 7
- 6 Face ventrale entièrement mouchetée de clair sur fond sombre *L. ovatus ovatus*
 Gorge seule mouchetée de clair sur fond ombre, le reste de la face ventrale rose in vivo, avec de rares ponctuations *L. ovatus orientalis*
- 7 Face ventrale entièrement couverte de vermiculations noires et blanches; fascie dorsale peu apparente, réduite à un petit triangle céphalique *L. ventrimarmoratus*
 Face ventrale entièrement claire, rose ou jaunâtre in vivo, sauf la gorge, foncée; fascie dorsale assez nette, en triangle étiré jusqu'au milieu du dos *L. boulengeri*
- 8 Gorge des mâles présentant de gros plis paramandibulaires ou sac vocal très développé, pas d'hypertrophie brachiale ni de spinosité pectorale, 2, 3 ou 4 épines métacarpiennes chez le mâle 9
 Pas de plis gulaires chez les mâles, spinosité pectorale très développée, hypertrophie brachiale et 5-6 épines métacarpiennes chez le mâle (*L. polyacanthus*) 11
- 9 Taille moyenne 26 mm chez les mâles, dessous, sauf la gorge, d'un rose saumon uniforme, gorge des mâles présentant de gros plis paramandibulaires, pas d'hypertrophie brachiale ni de spinosité pectorale, 2 ou 3 épines métacarpiennes chez le mâle (*L. albiventris*) 10
 Taille du seul mâle connue 22 mm, dessous brun avec vermiculations blanches, sac vocal très développé chez les mâles, pas d'hypertrophie brachiale ni de spinosité pectorale, 3 épines métacarpiennes *L. blanchi*

- 10 Orteils munis de prolongements acuminés souples; dessus entièrement sombre sauf 2 fascies paranales oranges; 2 épines métacarpiennes chez le mâle *L. albiventris albiventris*
 – Orteils sans prolongements; partie postérieure du dos, base des cuisses, moitié distale des jambes et base des tarses éclaircis, beige in vivo, 3 épines métacarpiennes chez le mâle *L. albiventris bueanus*
11. Face ventrale plus ou moins assombrie, mais dépourvue de points ronds éclaircis (bleutés in vivo); triangles d'épines pectorales larges, ne se joignant pas sur le milieu de la poitrine
 *L. polyacanthus polyacanthus*
 Face ventrale ponctuée de clair sur un fond assombri, triangles d'épines pectorales étroits, se joignant sur le milieu de la poitrine *L. polyacanthus punctiventris*
12. Face dorsale bi- ou tricolore, face ventrale noire avec de grosses taches blanches arrondies ou bacilliformes, pas de protubérances axillaires, pas d'hypertrophie brachiale, 2-3 épines métacarpiennes chez le mâle (groupe de *L. bicolor*) *L. bicolor*
 – Face dorsale en générale unicolore (ou mouchetée. *L. axillaris*), face ventrale non tachée de blanc sur fond noir; des protubérances axillaires et une forte hypertrophie brachiale chez le mâle (groupe de *L. mertensi*) 13
- 13 Dessus brun foncé (mâles) ou rouge ou rougeâtre (femelle); dessous vivement coloré avec pigment rouge plus ou moins étendu; 3-4 épines métacarpiennes chez le mâle 14
 – Pas de dichromatisme sexuel; dessous blanchâtre avec taches nébuleuses sombres plus ou moins étendues, aucun pigment rouge; 2 ou 5-6 épines métacarpiennes chez le mâle 15
- 14 Dessus à pigmentation très contrastée, en général blanc avec grosses marbrures noires et bords rouge vif *L. mertensi*
 – Dessous finement moucheté de brun noir sur fond rougeâtre, rosé ou blanchâtre (mâles) ou rouge cerise ou rouge et blanc (femelles) *L. erythrograster*
15. Taille petite (moyenne des mâles. 23 mm, femelles. 28 mm); dessus brun ou roussâtres sans taches jaunes; tegument peu granuleux, protubérances axillaires subconiques et 2 épines métacarpiennes chez le mâle *L. perreti*
 Taille grande atteignant 38 mm chez les mâles qui sont plus grands que les femelles (27-33 mm), dessus brun violace foncé, avec souvent des mouchetures jaunes, tegument très granuleux dorsalement, protubérances axillaires aplaties et tronquées et 5-6 épines métacarpiennes chez le mâle *L. axillaris*

Corresponding editor: John C. POYNTON.

Miscellanea nomenclatorica batrachologica.

19. Notes on the nomenclature of Ranidae and related groups

Alain DUBOIS

Laboratoire des Reptiles et Amphibiens, Muséum national d'Histoire naturelle,
25 rue Cuvier, 75005 Paris, France

The need of "working taxonomies", as tools providing a framework for alpha-taxonomic revisionary works and hypotheses for phylogenetic analyses, is pointed out, especially in groups with wide distribution and high number of species. Even during the transitional period, non-ambiguous communication between zoologists requires that use of names for taxa strictly follows the international rules of zoological nomenclature. Several cases of recent nomenclatural problems are pointed out in the "family Ranidae". Rediscovery of the generic name *Chilixalus* Werner, 1899 provides an opportunity for discussing several careless treatments of the generic and infrageneric taxonomy of frogs of the "genus *Rana*" by recent authors. The name *Indiraninae* Blommers-Schlösser, 1993 is shown to be an invalid junior synonym of *Ranixalinae* Dubois, 1987, and, on this occasion, the fact that family-group names are regulated by the rule of priority is reminded once again. In order to help knowing the valid name among several names published simultaneously, in the case they are considered subjective synonyms, two tables of first-reviser actions in the Ranidae and related groups are presented. Finally, discussion of the nomenclatural status of the name "*Rana duboisi*" recently published by EMERSON & WARD (1998) allows to point to the problems posed by the publication of data taken from unpublished manuscripts by colleagues, either submitted to review by an editor, or privately communicated by the author or another person. This case is also the basis for the discussion of two more general questions, which are likely to appear again on several occasions in the years to come: is a species name rendered nomenclaturally available by publication, either (1) of a Genbank catalogue number, or (2) of a cladogram including this species? The answer to both questions is clearly "no", at least under the current Code. Allocation of names to taxa is not based on definitions, diagnoses or descriptions, but on the taxonomic allocation of name-bearing type-specimens: the recent proposal of attaching the names to "phylogenetic definitions of taxon names" is therefore based on a major misunderstanding and entertains an unnecessary confusion between taxonomy and nomenclature, as the current nomenclatural system is liable to accommodate any kind of taxonomy, including "phylogenetic" ones.

With more than 750 species (GLAW et al., 1998) distributed almost worldwide, the "family Ranidae" is one of the largest amphibian higher taxa. Its taxonomy is still very problematic, if not really "in a state of chaos" (DUELLMAN & TRUEB, 1985: 544). Resolution of all the problems it raises will be a long task, as it will require a high number of works of

various kinds (morpho-anatomical, molecular, cytogenetic, bioacoustic, ethological, ecological), both at local scale and at world scale, and dealing both with alpha-taxonomy and with higher classification. Only when this is done can we hope to have a reasonably good knowledge of the species of the family and understanding of their phylogenetic relationships. Given the high number of species concerned, and the extremely large distribution of the group, it is impossible for any researcher to work on the whole of the family at once. Before applying any technique or carrying out any survey, choices must be made among the hundreds of species of the family. This choice can be made along three major lines: (1) on a geographical basis, i.e. studying the ranids of a given region of the world; despite the fact that this approach is clearly unsatisfactory (see e.g. DUBOIS, 1981, 1987a, 1992), for material reasons this has been the case of the vast majority of works dedicated to the taxonomy of this family until now; (2) according to the availability of specimens in one or several museum or other collection(s), which may be a little better when rich, largely representative collections are used, but remains unsatisfactory in most cases; (3) on a provisional taxonomic basis, which is clearly the best starting point for any revisionary taxonomic work (see e.g. MAYR, 1981). Some zoologists (e.g., INGER, 1996) seem to think that a taxonomy is only a *result*, and that taxonomies should only be established, or changed, when biologists have "final" data on the (cladistic or other) relationships between the species. This is a very reductory and misleading view of the rôle of taxonomy in biology, for two reasons at least:

(1) Most data on which taxonomies are based are conventional (i.e., based on subjective choices, e.g. as to which kind of information should be provided by the classification) and/or hypothetical (e.g., cladograms as hypotheses of cladistic relationships). As a consequence, no taxonomy is or will ever be the "final" one, for any group of living beings. Asking to postpone the establishment or change of taxonomies until we have "final" data is just a way to say that no taxonomy can ever be established, or that the existing taxonomies (often inherited from "tradition", both in its best and worse senses), should never be changed, for reasons of "stability of nomenclature". However, no nomenclature can ever be completely stable, if taxonomy is to remain a living, i.e. evolutive, science (see DUBOIS, 1998).

(2) Such requests ignore one of the functions of taxonomies, i.e. their "heuristic value": a taxonomy is not only a result, it is also a *starting point*. It is a hypothesis, that can be tested by further research and modified. This is particularly true in speciose and complex groups with large distributions, that cannot be comprehensively studied at once, such as the Ranidae: in these groups, at least if one really wishes to improve the existing taxonomies, provisional groupings as "phenetic taxa" (such as e.g. the "phenetic groups" recognized in toads of the genus *Bufo* by some authors: DUFLMAN & SCHULTE, 1992, DUBOIS & OHLER, 1999) are necessary to have a "working taxonomy". Such groups of a reasonable size, chosen neither on a geographical nor on "availability" grounds, will allow real, although partial, revisionary works. This is demonstrated by the fact that most of those who recently really tried to improve the taxonomy of ranids above the species level (and not only to "comment" on the work of others), had to start from subsets of the whole family, which, although they might not have stated it, were those proposed as "working taxa" by previous authors (see e.g. EMERSON & BERRIGAN, 1993; EMERSON, 1996; EMERSON & WARD, 1998)

The request for stability of taxonomies and nomenclatures, that some authors (e.g. INGER, 1996) wish to apply to the Ranidae¹, is relevant only for some zoological groups, either of very small size (e.g., higher primates) or already very much studied (e.g., birds), for which an enormous wealth of information is already available, and in which competing taxonomic schemes only or mostly depend on subjective choices as to the major criteria to be taken into account in the building of classifications (classification or "cladification". MAYR, 1997; DUBOIS, 1997), on different weightings of the characters, etc. But in poorly known groups like the Ranidae, we strongly need provisional, working taxonomies, to really help progress of research and to guide future alpha-taxonomic works and phylogenetic studies. Such temporary taxonomies can be progressively modified and replaced by better ones, as information becomes available, but just to obtain this information may be very time-consuming. Pending its obtention, zoologists cannot be left in a "non-taxonomic land". They need "working taxonomies" and "working nomenclatures". In such groups, a fascination, or a quasi-religious respect, for "stability" of taxonomy and nomenclature, can work as a break against increase and improvement of our knowledge. Of course, in such enormous groups as the Ranidae, where no researcher in the world can have access to all, or even to a high proportion of, the described species, and where many species are known only by a very low number of specimens, sometimes only in the adult stage (the tadpoles being unknown), such a provisional taxonomy can only be based on a heterogeneous combination of various sources of information: some based on field work, some on detailed anatomical studies, some on examination of specimens limited to external characters, and some on data published by previous authors. Because of this unavoidable diversity of sources of information, the data set is bound to be incomplete, as some character states (particularly those requiring dissection and anatomical study, or those of tadpoles) will be known for some taxa only: such data cannot therefore be used to build up a matrix and carry out a phylogenetic analysis, but can allow partial, provisional definitions of phenetic groups, diagnosed by characters shared only by their included species and that can in a first step be hypothesized to be synapomorphies of the latter. Of course, such a work is likely to include some mistakes, but then a useful contribution of subsequent workers will be to correct these and improve the provisional

¹ Actually, the motivation for writing this paper (INGER, 1996) are difficult to understand. Although this author has published numerous papers on the Oriental, Asiatic and African frogs for more than half a century, he has never shown real interest in the phylogeny and supraspecific taxonomy of these groups, as he never provided a significant contribution to this field but merely perpetuated BOULENGER's ideas and schemes in this respect. Some of the information provided in his recent paper could have been proposed as a constructive contribution to the taxonomy of ranids, and will, no doubt be used as such in the future. This is indeed the kind of information I was expecting when I wrote my "proposals" (DUBOIS, 1992), which are clearly a basis for discussion and improvements, not a "final system": although my paper was the result of research over a 20-year period, it is clear that I could not have examined all ranid groups worldwide. However, instead of proposing these comments as positive elements for correcting and improving my proposals, INGER's (1996) paper is only negative and aggressive, and does not offer alternate proposals but "waiting for more data", to paraphrase KOTTELA's (1997: 4) nice words (see also DUBOIS & OHLER, 1999: 135). This casts some doubts on the real intentions of its author (and of the editors of the journal where it was published). The aim of this publication was clearly not to open a debate (which could well have been published in the "points of view" of this journal) this way I did not think it worthwhile to write a reply. Replies will come slowly but surely as the much needed works on the ranids are progressing (see e.g. MARMAYOU et al. in press). In the meantime, following INGER's "traditional" taxonomy is not likely to help authors who are really interested in the relationships within the Ranidae, and who need subgroups to deal with the hundreds of species still allocated by some to the genus *Rana* presenting these species in a publication by alphabetical order of specific names is highly misleading, as is the use of arbitrary groups based on grossly incomplete data, as well exemplified by the recent "sections" recognized by TIAN et al. (1995) in this genus, which ignore many important pieces of information published after BOULENGER's works.

taxonomy, rather than reject it altogether without using its good parts. This is the way science usually progresses, particularly in biology (see e.g. MAYR, 1982, 1997).

Taxa, even provisional, must be named (DUBOIS, 1988), and the fact that they are provisional does not mean that their nomenclature should not be rigorous. Strictly following the rules of the *International Code of Zoological Nomenclature* (ANONYMOUS, 1985; quoted below as "the Code") is a guarantee of *non-ambiguous, stable, automatic and universal allocation of names to taxa*, which is much more important than the (highly praised by some) "stability of taxa and names". Among these rules, the rule of priority is an important one. A recent tendency has developed among some zoologists (e.g., SAVAGE, 1990a-b, 1991; BOCK, 1994) and in decisions of the International Commission on Zoological Nomenclature (quoted below as "the Commission") to severely limit its application in zoology. In so doing, the Commission has not properly played its rôle of "Keeper of the Law" (DUBOIS & OHLER, 1997: 299), and has encouraged neglect of all the rules by zoologists. No doubt such attitudes contribute to the current weakening of the binding legislative status of the *Code* for the establishment of the valid names of taxa in the eyes of many taxonomists. Such a movement may have important negative consequences in the long run regarding the existence of a unique international nomenclatural system, and therefore the unity and universality of zoology as a science (DUBOIS, in preparation).

In the recent years, and largely as a result of this tendency, a number of nomenclatural problems in amphibians have been pointed out (see e.g. DUBOIS, 1987a-b, 1995, 1998, DUBOIS & OHLER, 1995, 1998). The purpose of this paper is to present a few new such problems in the Ranidae and their solutions, within the frame of the current taxonomy of this family. This does not preclude the possibility that the nomenclature of the taxa discussed below may have to be changed in the future, as the taxonomy of these groups evolves. Nomenclature being at the service of taxonomy (and not the reverse), names will necessarily have to change as taxa are modified, suppressed or created. The particular cases presented below will also provide the opportunity to discuss several more general problems of zoological nomenclature and of scientific publications.

CHILIXALUS WERNER, 1899

SCHMIDT (1857: 11) published a preliminary diagnosis of *Ixalus warszewitschii*. Shortly after, the same author (SCHMIDT, 1858: 241-242, 258, pl 1) provided a more detailed description of this species, for which he gave a precise type-locality, now situated in Panama (see HILLIS & DE SÁ, 1988: 15). For the name of the species, he then used two spellings: on page 258, the correct original spelling *Ixalus warszewitschii*, and on page 241, on two occasions, the spelling *Ixalus warschewitschii*, which must therefore be viewed as an incorrect subsequent spelling, as noted by HILLIS & DE SÁ (1988: 16). Most subsequent authors (e.g., DUNN, 1931: 416, TAYLOR, 1952: 896; GORHAM, 1974: 153, FROST, 1985: 520) used this latter spelling, until HILLIS & DE SÁ (1988: 1) resurrected the correct original spelling.

SCHMIDT (1858: 242) stated that FITZINGER had privately suggested to him that this species should be placed in a new genus, but he refrained from doing so until field work could

bring more data about it. However, another, subsequent author did not have as many scruples and created a nominal genus for this species without having additional information: WERNER (1899: 117) proposed the new generic name *Chilixalus* for the nominal species "*Ixalus warszewiczii* Schmidt". He had apparently not seen the publications of SCHMIDT (1857, 1858) on this species, as he stated that he had found this name on a bottle in the Krakow Museum containing a frog specimen from "Neu Granada". Fortunately, he mentioned the collection number (1006) of this specimen, which is the same as that reported by HILLIS & DE SÁ (1988: 15) for SCHMIDT's (1857) holotype, so that there is no doubt about the fact that WERNER (1899) actually dealt with the same species as SCHMIDT (1857, 1858). WERNER's (1899) spelling of the specific name, repeated twice in his paper, was clearly intentional, and should be regarded either as an unjustified emendation of SCHMIDT's original name, or, because of WERNER's ignorance of SCHMIDT's publications, as the name of a new nominal species: in both cases, the name *Chilixalus warszewiczii* has an independent status in nomenclature and is a junior objective synonym of *Ixalus warszewitschu* Schmidt, 1857

Although published by a well-known zoologist in a major journal, the name *Chilixalus* has been almost completely forgotten by subsequent authors. It was mentioned by BOULENGER (1900b: 28; 1910: 152) and NEAVE (1939: 691), but ignored altogether in all major works dealing with the classification of Ranidae and Rhacophoridae, or with the ranids of Central America: e.g. GÜNTHER (1900), BOULENGER (1920), AHL (1931), NOBLE (1931), TAYLOR (1952), GORHAM (1974), DUBOIS (1981, 1992), DULLMAN & TRUBB (1985), FROST (1985) and HILLIS & DE SÁ (1988). Although close by its spelling to the generic names *Chirixalus* Boulenger, 1893 (Ranidae, Rhacophorinae) and *Callixalus* Laurent, 1950 (Hyperoliidae, Hyperoliinae), the name *Chilixalus* differs from these names by one or two letters, and is therefore not their homonym. The type-species of this nominal genus is now considered a member of the genus *Rana* Linnaeus, 1758, as *Rana warszewitschii* (Schmidt, 1857) (HILLIS & DE SÁ, 1988)

Fortunately, rediscovery of the name *Chilixalus* does not have disturbing effects on nomenclatural stability, whatever the classification scheme chosen. Three classification schemes are currently applied by different authors to the group of ranids including the nominal species *Ixalus warszewitschu* Schmidt, 1857: (1) for authors who do not recognize subgenera in *Rana*, it is a member of the *Rana palmipes* group; (2) for some authors, it is a member of the subgenus *Lithobates* Fitzinger, 1843 of *Rana*; (3) according to the provisional classification of ranids proposed by DUBOIS (1992), it is a member of the subgenus *Tryphlops* Cope, 1868 of *Rana*

Unfortunately, a certain amount of taxonomic and nomenclatural vagueness applies to several recent works dealing with the "*Lithobates* section" (DUBOIS, 1992: 323, 329) of the genus *Rana*. Although the title and abstract of their paper only referred to the "*Rana palmipes* group", HILLIS & DE SÁ (1988: 16-17) suddenly mentioned a "subgenus *Lithobates*", without stating its author, date and content, and without reference to a publication where this would appear. In support of this use, they gave two references, one to a paper (HILLIS & DAVIS, 1986) where the "subgenus *Lithobates*" was not at all mentioned, and one to an unpublished thesis (HILLIS, 1985), where a subgenus "*Lithobates* Fitzinger" (without date) was briefly mentioned (p. 266-267), without any reference allowing to identify this name. As a matter of fact, as of 1988, the status of the name *Lithobates* had been discussed in only one publication (DUBOIS,

1981: 249-250), not quoted by these authors, where this name was considered a synonym of *Rana*. Therefore, HILLIS & DE SÁ (1988) resurrected the generic name *Lithobates* for a new subgenus for which they did not provide a diagnosis, and without discussing, even briefly, the status of the other subgenera recognized until then in *Rana* (DUBOIS, 1981, 1987a).

The taxonomy of the American species, species-groups and subgenera currently referred to the genus *Rana* will not be definitively clarified until their relationships with non-American (i.e., European and East Asian) species of this "genus" are studied in detail, and any current taxonomic scheme can only be considered as a provisional, working taxonomy. I provide below synonymies of the subgenera provisionally recognized by DUBOIS (1992: 329-331) in his "*Lithobates* section" of the genus *Rana*: these are phenetically diagnosable groups for which a hypothesis of cladistic relationships has been proposed by HILLIS & DE SÁ (1988: 18). Under this scheme, the generic name *Chilixalus* appears as a junior subjective synonym of *Tryphteropsis*. Under the other classification schemes mentioned above, it is either a junior subjective synonym of *Lithobates* or a junior subjective synonym of *Rana*.

Lithobates Fitzinger, 1843

- Lithobates* Fitzinger, 1843: 31 Type-species by original designation: *Rana palmipes* Spix, 1824: 29
Ranula Peters, 1859: 402 (nec Schumacher, 1817: 77) Type-species by monotypy: *Ranula gollmeri*
 Peters, 1859: 402.
Pohlia Steindachner, 1867: 15 Type-species by monotypy: *Rana palmipes* Spix, 1824: 29

Sierrana Dubois, 1992

- Sierrana* Dubois, 1992: 330. – Type-species by original designation: *Rana sierramadrensis* Taylor, 1939: 385

Tryphteropsis Cope, 1868

- Tryphteropsis* Cope, 1868: 117 Type-species by original designation: *Ranula chrysopravina* Cope, 1866: 129
Levirana Cope, 1894: 197 Type-species by monotypy: *Levirana vibicaria* Cope, 1894: 197
Chilixalus Werner, 1899: 117 Type-species by monotypy: *Chilixalus warszewitschii* Werner, 1899.
Laevirana Gunther, 1900: 206 – Unjustified emendation of *Levirana* Cope, 1894.

Zweifelia Dubois, 1992

- Zweifelia* Dubois, 1992: 330 – Type-species by original designation: *Rana tarahumarae* Boulenger, 1917b: 416

OTHER INCONSISTENCIES IN RECENT TREATMENTS OF RANID TAXONOMY
AT GENUS AND SUBGENUS LEVEL

The case of the "subgenus *Luthobates*" just discussed is not unique in the recent literature dealing with ranid taxonomy. To tell the truth, it is difficult in many cases to be sure of what infrageneric taxonomy is indeed followed by many current authors within the genus *Rana*, which clearly points to a general uneasy feeling in this respect. Thus, in a paper dealing with some Asian frogs, EMERSON & BERRIGAN (1993) mentioned a "subgenus *Limnonectes* (Fitzinger)" in their title, but did not clearly state in the text which species they included in this subgenus, nor in other "subgenera" of their very comprehensive "genus *Rana*". They introduced (p. 23) the new combination "*Rana (Occidozyga) cyanophlyctus*" without any comment, which seems to imply that they recognized a new subgenus *Occidozyga* in the genus *Rana*. However, they did not propose a diagnosis or definition of the latter, nor did they define its content. Did they mean that all species shown in the consensus tree of their figure 8 should be included in this subgenus, or should the latter be understood as comprising only some species of this tree, namely *luna* (type-species of *Occidozyga*: see DUBOIS, 1981), *limnocharis*, *cancrivora* and *cyanophlyctus*? This information is not to be found in their paper. It is surprising to see publication of such non-professional treatments of taxonomic and nomenclatural matters in a well-known herpetological journal, but this is only one example of a recent tendency for zoological publications, even of high level, to ignore the basic taxonomic and nomenclatural rules.

In a later paper, EMERSON (1996: 279) first expressed high concern for the proper use of scientific names in biological publications. "until a proper systematic treatment is completed, it seems premature and potentially confusing to use the name *Limnonectes* in the literature. In this paper, members of that group will be referred to as the fanged frogs and their relatives." However, a few pages below in the same article, she seemed to have forgotten these good resolutions, as she presented quite confusing information. In page 281, she wrote. "Egg size was measured in adult females of 19 species of fanged frogs and 16 species of outgroup ranids belonging to the genus *Hylarana*". In the legend of her figure 2 (p. 282), "outgroup species of the genus *Hylarana*" appear again, but the text of the same page mentions "outgroup ranids belonging to the subgenus *Hylarana*". Genus or subgenus? Actually, until now, while most zoologists working in Africa consider *Hylarana* Tschudi, 1838 as a genus, no author working on Asian frogs has treated *Hylarana* as a full genus, except FIE et al. (1991) and YE et al. (1993), in two works not cited in the *References* of EMERSON'S (1996) paper, so that treating Oriental *Hylarana* as a full genus would seem to have required at least a short comment. Furthermore, DUBOIS (1987a: 42) pointed out that Asian species of "*Hylarana*" did in fact represent several clearly distinct groups, and later (DUBOIS, 1992) distributed these species in several sections and subgenera of the genus *Rana*. It would therefore be important to know which are the "16 species of outgroup ranids belonging to the genus *Hylarana*" studied. Unfortunately, EMERSON'S (1996) paper does not contain a list of the species, not to say of the specimens, examined. Contrary to her initial statement, EMERSON'S (1996) taxonomic treatment of the Ranidae is very difficult to understand and highly confusing. On one hand, she recognized a genus (or subgenus?) *Hylarana* distinct of *Rana* for a heterogeneous group of frogs that by all skeletal and morphological characters have long been known to be rather closely related to the group including the type-species of *Rana* (*Rana temporaria* Linnaeus, 1758). But on the other hand,

allegedly to avoid "potential confusions" linked to the use of the name *Limnocytes*, she maintained in *Rana*, without comment and without mention of subgenera, several groups of ranids long known to be only distantly related to the latter group, including some that have been for more than 150 years (since TSCHUDI, 1838) placed in one or two genera (*Occidozyga* Kuhl & Van Hasselt, 1822 and sometimes *Phrynoglossus* Peters, 1867) distinct from *Rana*. All these taxonomic and nomenclatural novelties were presented in this paper without explanation or discussion, and published in a famous journal whose title claims interest in "systematic biology".

INDIRANINAE BLOMMERS-SCHLÖSSER, 1993 AND NYCTIBATRACHINAE BLOMMERS-SCHLÖSSER, 1993

I have on several occasions already (e.g., DUBOIS, 1984: 6, 1987b, 117-126, 1987c, 48-52) pointed out that, contrary to what some zoologists seem to believe, family-group names in zoology are regulated by the *Code* and must follow the rule of priority, just like species-group and genus-group names. This means in particular that the valid name of a family-group taxon is the first published one based on a generic name included in the taxon, whatever the current status of this generic name (valid name or invalid junior synonym), this is exactly parallel to the situation in the genus-group, where a genus name can be valid even if its type-species is a junior synonym. This rule is by far the best one for the stability of names, for reasons that were explained in detail already by MYERS & LEVITON (1962), and that may be well illustrated by a simple example (see DUBOIS, 1984). GÜNTHER (1858) established a family Polypedatidae, based on the generic name *Polypedates* Tschudi, 1838. This family was recognized under this name by many authors for many years, including in the title of a volume of the famous series *Das Tierreich* (AHL, 1931), but its name was changed into Rhacophoridae by HOFFMAN (1932) because the genus *Polypedates* was then considered a synonym of *Rhacophorus* Kuhl & Van Hasselt, 1822. Since then however, a tendency has developed to revalidate *Polypedates* as a valid genus it would clearly have been better, for the sake of nomenclatural stability, to keep using the name Polypedatidae for the family, whatever the status of the generic names. A quite similar case concerns the use of Microhylidae Günther, 1858 instead of Gastrophrynidae Fitzinger, 1843 (see DUBOIS, 1984). In both these cases, by virtue of Article 40 of the *Code*, the senior names (Polypedatidae and Gastrophrynidae) cannot be resurrected now, as they were replaced because of a synonymy of the type-genus before 1961, but it is important to note that the same would not be true if this replacement had taken place after 1960.

A number of recent authors do not understand this rule, or deliberately refuse to follow it, and they tend to change the name of a family group taxon as soon as its type-genus is considered an invalid junior synonym, even when this was first done much after 1960; they may even clearly argue in favour of this non-respect of the *Code* (see e.g. SAVAGE, 1986). Strikingly, in several recent cases, their attitude was supported by the Commission itself, in accepting to "suppress" some senior synonyms in the family-group in order for the corresponding taxa to bear names based on valid generic names. If followed by all, this movement would lead to suppress the rule of priority for family-group names, thus going back to a situation where local groups of zoologists, the most "powerful" ones probably, could try and

impose "their" nomenclature to the whole international scientific community – a most retrograde step indeed.

Interested readers can find a list of such problems in living amphibian family-group nomenclature in DUBOIS (1984, 1987a: 11-12, 1987b 121-122, 1987c 48-52). Particularly striking are the cases of two invalid names that are still used by some authors (and accepted by the editors of some journals, even well-known ones), despite these repeated mentions of their invalidity, and although in these cases Article 40 does not apply and does not permit to keep them, i.e. the invalid *Xenopodinae* Fitzinger, 1843 instead of the valid *Dactylethrinae* Hogg, 1838, and the invalid *Bombininae* Fejérváry, 1921 instead of the valid *Bombinatorinae* Gray, 1825.

I here wish to point out a new case of the same kind DUBOIS (1987a: 66) established a tribe *Ranixalini* for the ranid genera *Nannophrys* Gunther, 1869, *Nyctibatrachus* Boulenger, 1882 and *Ranixalus* Dubois, 1986. Some months later, however, the same author (DUBOIS, 1987d) discovered that the generic name *Indirana* Laurent, 1986 was a senior subjective synonym of *Ranixalus* and should replace it; however, he remarked that, according to the *Code*, the name *Ranixalini* did not have to be changed and remained the valid one for the tribe. DUBOIS (1992: 334) raised this tribe to the rank of subfamily, under the name *Ranixalinae*. BLOMMERS-SCHLÖSSER (1993) presented a new hypothesis of cladistic relationships within the *Ranidae* and proposed two new subfamilies, the *Indiraninae* and the *Nyctibatrachinae*. The first of these names is clearly an invalid one, being a strict junior subjective synonym of *Ranixalinae*: if subsequent authors wished to adopt BLOMMERS-SCHLÖSSER's (1993) taxonomic scheme, they should replace the name *Indiraninae* by *Ranixalinae* in this classification. As for the name *Nyctibatrachinae*, it is also likely to be a synonym of *Ranixalinae*, but here for taxonomic, not nomenclatural, reasons. BLOMMERS-SCHLÖSSER (1993) did not take into account in her analysis the characters pointed out by DUBOIS (1987a, 1992) and that suggest that *Indirana*, *Nannophrys* and *Nyctibatrachus* most likely constitute a holophyletic group, such as the presence of femoral glands in males of *Indirana* and *Nyctibatrachus*, the highly derived terrestrial tadpoles showing several probable synapomorphies in *Indirana* and *Nannophrys*, and the characters shared by *Nannophrys* and *Nyctibatrachus* according to CLARKE (1983: 395). Despite these data, BLOMMERS-SCHLÖSSER (1993) referred these three South Indian and Sri Lankan genera to three distinct subfamilies (she included *Nannophrys* in her African subfamily *Cacosterninae*). Therefore, the whole phylogenetic, taxonomic and nomenclatural scheme proposed by this author seems highly questionable and will have to be re-evaluated.

RELATIVE PRIORITY BETWEEN SIMULTANEOUS NAMES

As shown by these examples, it is clear that the taxonomy of the *Ranidae* is still not stabilized and will show important changes in the future. As argued above, the existence of provisional taxonomic schemes, if well understood, can provide a strong help for the progress of our works on this taxonomy. Taxonomic changes will in their turn result in nomenclatural changes, but, if the proper care is taken, these latter changes will be automatic and should not pose any problem to taxonomists. The previously published catalogues of genus-group and

Table 1 - Past first-reviser actions concerning simultaneous (i.e., published at the same date) genus-group and family-group names in the families Hyperolidae, Phrynobatrachidae and Ranidae (as defined by DUBOIS, 1992). The sign > means "afforded priority over"

Original publication	First-reviser	Relative priority afforded to simultaneous names by first-reviser action
TSCHUDI, 1838	DUMÉRIE & BIBRON, 1841 515	<i>Polypedates</i> > <i>Boophis</i> + <i>Buergeria</i>
TSCHUDI, 1838	STEINER, 1907 143	<i>Polypedates</i> > <i>Buergeria</i> + <i>Theioderma</i>
FITZINGER, 1843	FITZINGER, 1843 31	<i>Pelophylax</i> > <i>Euphyctis</i> + <i>Limnophilus</i> + <i>Phrynomerina</i>
FITZINGER, 1843	DUBOIS, 1976 1112	<i>Euphyctis</i> > <i>Limnonectes</i> + <i>Phrynomerina</i>
BOULENGER, 1882	DUBOIS, 1987a 68	<i>Nyctibatrachus</i> > <i>Nannobatrachus</i>
NOBLE, 1931	DUBOIS, 1982, 135-136	<i>Petropedetmae</i> > <i>Cacosternum</i>
LAURENT, 1944	LAURENT & COMBAZ, 1950 277	<i>Afrizalus</i> > <i>Acanthizalus</i> + <i>Heterizalus</i>

family-group names available in the Ranidae (DUBOIS, 1981, 1984, 1987a, 1992) should allow any author to find if names are already available for any newly defined taxon, which one has priority, or if a new name has to be coined. The only cases when nomenclatural changes will not be automatic are those where different names, initially published in the same work or in different works but at the same date ("simultaneous names"), are considered subjective synonyms. In such cases, according to the *Code*, relative priority among these names is fixed by a first-reviser action. Once published, a first-reviser action is definitive and cannot be modified by subsequent authors. It is therefore important to be able to trace all first-reviser actions ever taken in the nomenclature of a given zoological group, but it is a difficult work for anyone who is not very well acquainted with all the literature dealing with the taxonomy of the group.

In order to help future workers on the taxonomy of Ranidae and related groups (recognized as the families Arthroleptidae, Astylosternidae, Hemisotidae, Hyperolidae, Mantellidae and Phrynobatrachidae by DUBOIS, 1992: 309), I provide in tab. 1-2 a list of publications where several simultaneous genus-group and family-group names currently referred to these groups were published, with information on first-reviser actions and on the resulting relative priority among these names. Only names created in the same publication were surveyed. Problems of priority may also occur between names published in different works of the same year, but then a careful study of the case, with research of information on exact dates of publication, must be carried out, which was beyond the scope of the present work. Table 1 gives information on first-reviser actions that have already been taken by previous authors in the past. When no such first-reviser action has already been published, I hereby take such an action (tab. 2), so that in the future any allocation of genus-group or family-group name in these families should be automatic (except in the rare possible cases of names published in different works of the same year, as mentioned above) and not liable to be complicated by subsequent "madvertent" first-reviser actions in obscure publications (e.g., due to subjective synonymisation of two names, one being cited in the synonymy of the other) that may escape the attention of some colleagues. The choice of the order of priority among

Table 2 New first-reviser actions concerning simultaneous (i.e., published at the same date) genus-group and family-group names in the families Arthroleptidae, Astylosternidae, Hemisotidae, Hyperoliidae, Mantellidae, Phrynobatrachidae and Ranidae (as defined by DUBOIS, 1992) The sign > means "afforded priority over" Names followed by an asterisk were also concerned by past first-reviser actions (see tab 1), in such cases, the new first-reviser actions below are compatible with these earlier actions.

Original publication	Relative priority afforded to simultaneous names by present first-reviser action
KUHL & VAN HASSELT, 1822	<i>Rhacophorus</i> > <i>Occidozyga</i>
TSCHUDI, 1838	<i>Hylarana</i> > <i>Polypedates</i> * > <i>Boophis</i> * > <i>Pyxicephalus</i> > <i>Buergeria</i> * > <i>Strongylopus</i> > <i>Theلودerma</i> * > <i>Cornufer</i> > <i>Oxyglossus</i> > <i>Eucnemis</i> > <i>Orchestes</i> > <i>Oxydozyga</i>
DUMÉRIEL & BIBRON, 1841	<i>Tomopterna</i> > <i>Limnodytes</i> > <i>Ixalus</i>
FITZINGER, 1841	<i>Pelophylax</i> * > <i>Euphlyctis</i> * > <i>Limnocoetes</i> * > <i>Lithobates</i> > <i>Hydrophylax</i> > <i>Tachycnemis</i> > <i>Trachyhyas</i> > <i>Eremophilus</i> > <i>Limnophilus</i> * > <i>Phrynoderma</i> *
GISTEL, 1848	<i>Philautus</i> > <i>Zoodoetes</i> > <i>Buccinator</i> > <i>Denarcus</i> > <i>Phyllodytes</i> > <i>Epipole</i>
SMITH, 1849	<i>Arthroleptis</i> > <i>Stenorhynchus</i>
GÜNTHER, 1859	<i>Platymantis</i> > <i>Leptopelis</i> > <i>Hemisus</i> > <i>Sphaerotneca</i>
PETERS, 1863	<i>Hoplobatrachus</i> > <i>Hemumantis</i> > <i>Leptoparus</i>
COPE, 1865	<i>Amolops</i> > <i>Staurois</i>
PETERS, 1867	<i>Phrynoglossus</i> > <i>Leptomantis</i>
GÜNTHER, 1869	<i>Nannophrys</i> > <i>Megalixalus</i>
HOFFMANN, 1878	<i>Fergusonia</i> > <i>Aemolops</i> > <i>Crummifera</i>
BOULENGER, 1882	<i>Mantella</i> > <i>Nyctibatrachus</i> * > <i>Nannobatrachus</i> *
SCHULZE, 1890	<i>Crotaphitis</i> > <i>Baliopygus</i>
BOULENGER, 1893	<i>Chirixalus</i> > <i>Phrynoderma</i>
PALACKY, 1898	<i>Rhacoforus</i> > <i>Nannophrys</i>
BOULENGER, 1900a	<i>Trichobatrachus</i> > <i>Cardioglossa</i> > <i>Scotobleps</i> > <i>Gampsosteonyx</i> > <i>Dilobates</i>
BOULENGER, 1917a	<i>Psychadena</i> > <i>Aubria</i>
METHUEN, 1920	<i>Gephyromantis</i> > <i>Trachymantis</i>
AHL, 1924	<i>Pseudocassina</i> > <i>Tormerella</i>
AHL, 1925	<i>Hylarthroleptis</i> > <i>Pararthroleptis</i>
HEWITT, 1926	<i>Arthroleptella</i> > <i>Microbatrachella</i> > <i>Microbatrachus</i>
AHL, 1927	<i>Palmatorappia</i> > <i>Dendrobatorana</i>
NOBLE, 1931	<i>Petropedetinae</i> * > <i>Cacosterninae</i> * > <i>Cornuferrinae</i> > <i>Phrynosipinae</i>
DECKERT, 1938	<i>Micrarthroleptis</i> > <i>Pseudarthroleptis</i>
LAURENT, 1940	<i>Caracodichus</i> > <i>Abrascophus</i> > <i>Arthrolepiulus</i>
LAURENT, 1941	<i>Taphromantis</i> > <i>Elaphromantis</i> > <i>Heteropelis</i>
LAURENT, 1944	<i>Afrixalus</i> * > <i>Heterixalus</i> * > <i>Acanthixalus</i> *
LAURENT & COMBAZ, 1950	<i>Cryptohylax</i> > <i>Phlyctimantis</i>
LAURENT, 1972	<i>Kassinini</i> > <i>Leptopelini</i>
DUBOIS, 1987a	<i>Ingerana</i> > <i>Kirtixalus</i> > <i>Toytorana</i> > <i>Amelia</i> > <i>Gorhixalus</i> > <i>Lurana</i> > <i>Bourretia</i>
DUBOIS, 1987a	<i>Ranixalini</i> > <i>Psychadenini</i> > <i>Tomopternini</i>
PERRET, 1988	<i>Alexiteron</i> > <i>Arlequimus</i> > <i>Chlorolus</i>
CHANNING, 1989	<i>Buergerunae</i> > <i>Tachycneminae</i>
FEI et al., 1991	<i>Odorrana</i> > <i>Glandrana</i> > <i>Rugosa</i> > <i>Pseudorana</i> > <i>Tenurana</i> > <i>Unculana</i> > <i>Quadrana</i> > <i>Tigrina</i>
DUBOIS, 1992	<i>Amo</i> > <i>Sylvirana</i> > <i>Nuhirana</i> > <i>Afrana</i> > <i>Amarirana</i> > <i>Ombrana</i> > <i>Sierrana</i> > <i>Nasirana</i> > <i>Pulchrana</i> > <i>Amerana</i> > <i>Pantherana</i> > <i>Humerana</i> > <i>Papurana</i> > <i>Sanguirana</i> > <i>Bommersta</i> > <i>Brygoomantis</i> > <i>Guibemantis</i> > <i>Spinomantis</i> > <i>Quasspa</i> > <i>Annandia</i> > <i>Eripaa</i> > <i>Gymandropaa</i> > <i>Ferana</i> > <i>Chalcorana</i> > <i>Aguarana</i> > <i>Zweifelia</i> > <i>Aurorana</i> > <i>Eburana</i> > <i>Tylerana</i>
DUBOIS, 1992	<i>Limnonectini</i> > <i>Paui</i> > <i>Conrauii</i>
BIOMMERS-SCHLOSSER, 1993	<i>Nyctibatrachinae</i> > <i>Indiraminae</i>
GLAW & VENCES, 1994	<i>Phylacomantis</i> > <i>Chonomantis</i> > <i>Pandoniscicola</i> > <i>Ochthomantis</i>

several simultaneous names was based on the following rationale: in most cases, names currently in use were afforded priority over names currently considered invalid, and well-known names over poorly known names; priority was usually given to names designating groups of larger size (with more species) than others, and to names designating genera over names proposed for subgenera; junior homonyms and objective synonyms (e.g., unjustified emendations) of potentially valid names were given lowest priority; all other things being equal, I have preferred euphonious or elegant names to disgraceful ones.

Of course, most of these first-reviser actions will have no bearing on future nomenclatures in these families, because synonymies between simultaneous names will be rather rare, even for the authors who currently advocate a very strong "lumper" approach to higher taxonomy: thus, to take just one example, it is highly unlikely that the names *Buergerinae* Channing, 1989 and *Tachycneminae* Channing, 1989 will ever compete for synonymy! However, in other cases the problem will certainly arise, and it will be simpler and easier to refer to a single couple of tables to know the relative situation of two given names, rather than having to embark on long and difficult researches, so that these tables embrace all cases of "simultaneous" family-group and genus-group names in these families.

"*RANA DUBOISI*" IN EMERSON & WARD (1998)

Peer review by colleagues before acceptance of a paper for publication in a scientific periodical or journal is now a common practice worldwide. Manuscripts thus submitted for advice to scientists, who usually work in the same research field as the author of the paper, are sent to them under the (usually tacit) agreement that the reader will not make a private use of the information contained in the paper and will not publish this information, or information derived from it, prior to the publication of the submitted paper. With some shocking exceptions, this rule is usually followed by reviewers. But a particular problem may arise when the submitted paper is rejected, at least in its original form, and is never published, or only published after a considerable delay. The risk exists that the referee, either by inadvertency or by lack of request for information, might consider that, after a certain time has elapsed, the paper was actually published, and might feel free to use the information it contained, or to refer to this information as if it had been published. In some cases, this merely has the consequence of publishing only the final result of a work, without all the accompanying data that allow to ascertain that these results were obtained in a serious scientific manner; in some other cases, this may have nomenclatural consequences.

An example of the first kind is KURAMOTO's (1990) mention of some of the results of a work by ISKANDAR et al. (unpublished) that he quoted as being in "*Alytes* (in press)", but that was actually never published or sent to press. The manuscript in question was indeed submitted to the journal *Alytes* on 4 April 1989, accessioned under number 89.156 and sent for review to two referees, including MITSURU KURAMOTO, on 12 April 1989. On 31 August 1989, after receipt of the reports of the two readers, copies of these reports were sent to the first author of the manuscript with an accompanying letter stating that, on the whole, the manuscript was very interesting and useful, but asking for a few minor modifications before

the paper could be published. Despite subsequent requests for the final manuscript, sent to the first author on 9 March 1990 and 18 October 1991, no second version of this paper was ever sent to *Alytes*. To the best of my knowledge, this paper was never published elsewhere. All the information contained in the original manuscript has therefore remained unpublished. Mention by KURAMOTO (1990) of some of this information is equivalent to mention of unpublished data obtained from a colleague through "personal communication", with the difference that in this case the communication was not direct between two colleagues, but went through the "mediation" of a journal editor. I suggest that colleagues who might wish to use these data should quote them as "ISKANDAR et al. in KURAMOTO (1990)".

In some cases, publication of previously unpublished taxonomic information may have nomenclatural consequences. This does not occur when no name is associated with the taxonomic information. Thus, EMERSON (1996: 279) wrote: "a new species has been discovered in Sulawesi in which the females retain fertilized eggs and the tadpoles develop in the body of the female (ISKANDAR, 1996)." This information seems quite interesting indeed, and readers may wish to know more about it. In the *References* of EMERSON's (1996) paper, the title of a paper by "ISKANDAR, 1996" appears, followed by the mention "*Alytes* (in press)". However, as of today (16 April 1999), no manuscript under this title (or an approaching one) has ever been submitted to *Alytes* for publication, so that this reference (ISKANDAR, unpublished a) could well be qualified as a "phantom reference" (see below). This may be quite frustrating for the reader but at least, from a nomenclatural point of view, there is no disturbing consequence, as the name of the "new species" was not mentioned.

The situation is different in the case of EMERSON & WARD's (1998) article on frogs of the "*Rana grunniens* species group". This paper starts (p. 538) with a table 1 presenting a list of species referred to this group. This table has a striking particularity: scientific names of species appear there "nude", i.e. without their authors and dates. As was well explained by NG (1994), citation of author and date is not only a tradition in zoology, it is important as it allows unambiguous identification of the nominal species at stake. Absence of such a basic information in a table published in a journal having "Linnean" in its title is an interesting illustration of a recent trend for zoological publications to neglect or fully ignore the basic rules, recommendations and needs of nomenclature. In this case, reference to DUBOIS's (1987a) work can allow the reader to avoid confusion, but without going to this reference it is impossible to know e.g. if the nominal species referred to in this table as "*Rana microtympanium*" is *Rana microtympanium* Van Kampen, 1907 (a member of *Limnodynastes*) or *Rana microtympanium* Boulenger, 1919 (a member of *Hildebrandtia*). This table contains 14 of the 15 names listed by DUBOIS (1987a: 63) as members of his *Limnodynastes* (*Limnodynastes*) *grunniens* group, but the name *Rana macrodon* has disappeared from this list without explanation. Transfer of all these species from the genus *Limnodynastes* to the genus *Rana* would have required a change of the grammatical gender of some of the specific names, which was not done in all cases, so that the list contains two incorrect spellings (*Rana modestus* for *Rana modesta*, *Rana visavanius* for *Rana visavama*). Later in the paper, p. 540, at the beginning of the *Material and methods*, two additional names suddenly appear for two species of this species-group: *Rana macrodon* and "*Rana duboisi*". This latter name is given without any explanation or reference to its source. It appears again on three occasions in the paper (p. 545, 546, 553), without further information. No publication proposing this name for a new species was ever published from 1758 to 1998, year of publication of EMERSON & WARD's (1998) work, so that

this name in this paper must be considered a new species name unless it was borrowed from some unpublished manuscript, not cited in the *References* of their paper.

Actually, I am aware of two unpublished manuscripts where this name, or a related one, was proposed as the name of a new species: in the first one (DAS, unpublished), the name "*Rana duboisi*" was proposed for a new species of *Rana* (*Sylvirana*) (sensu DUBOIS, 1992) from above Kallar (Kerala, India); in the second one (ISKANDAR, unpublished b), a new species of *Limnocytes* (*Limnocytes*) (sensu DUBOIS, 1992) from Kamarora (Lore Lindu National Park, Central Sulawesi, Indonesia) was described as "*Limnocytes duboisi*". To the best of my knowledge, none of these two papers has been published so far, and it is not even certain that they were ever submitted for publication. At the head of the manuscript of ISKANDAR's paper (a copy of which was presented to me by Georges PASTEUR), it was stated that this paper was intended for submission to the journal *Alytes*, but as of today this has not yet been done. However, it is very likely that the name "*Rana duboisi*" was borrowed (and modified, through change of generic allocation) from this second manuscript, as the origin given for the specimens of this species studied by EMERSON & WARD (1998: 553) is the same (except for the misspelling "Linu" for Lindu) as that of the type-locality of "*Limnocytes duboisi*" in ISKANDAR (unpublished b), and as EMERSON & WARD (1998: 551) thank Djoko ISKANDAR for providing them with "tissue samples of Southeast Asian ranids". It would thus appear that EMERSON & WARD (1998), by publishing the name "*Rana duboisi*" before ISKANDAR, became the authors (in the technical sense of this term according to the *Code*) of this nominal species. However, this is not true, because this name is a nomen nudum in their paper: no character is provided to distinguish this species from related ones, nor is there any reference to a "bibliographic reference to such a published statement" (Article 13 a of the *Code*). This case is interesting, however, as it allows discussion of two questions that are likely to be raised again later in zoological nomenclature: is a species name rendered nomenclaturally available by publication, either (1) of a Genbank (or other similar data base) catalogue number reference for a sequence of this species, or (2) of a cladogram showing the hypothesized relationships of this new species to related taxa?

(1) EMERSON & WARD's (1998) paper does not contain any table or figure giving the sequences obtained for portions of the 12S and 16S ribosomal RNA genes of the specimens studied in their work. If it was the case, the sequences associated with the new name "*Rana duboisi*" would clearly qualify as diagnostic characters making this latter name nomenclaturally available, just like mating call characteristics (see e.g. SCHNEIDER & SINSCH, 1992; DUBOIS & OHLFR, 1995: 179) or any other non-morphological character of an animal species. EMERSON & WARD (1998: 541) stated that the sequences obtained in their work were entered in the Genbank data base, and provided their catalogue numbers. As such a procedure is likely to become more and more common in evolutionary biology, it is important to know whether such Genbank cataloguing qualifies as a publication as defined by the *Code*. This is clearly not the case in the edition of the *Code* currently in force. Article 8 of this edition allows for a work containing a new name or a nomenclatural act to be regarded as published even if "produced after 1985 by a method that does not employ ink on paper in conventional printing", but only if it contains "a statement by the author that any new name or nomenclatural act within it is intended for permanent, public, scientific record". This does not apply to names entered in the Genbank, so that the latter must be considered as "unpublished" in the eyes of the *Code*. Caution will however have to be given to the precise wording of Article 8 in the final,

published version of the next edition of the *Code*, to check if this provision has not been changed. Sequences entered in the Genbank cannot therefore be used as diagnostic characters for new taxa, but it is important to note that, as soon as an author (either the person who established the sequence, or another colleague) publishes this sequence in a printed work, this sequence can become an excellent diagnostic character making a new name nomenclaturally available.

(2) Recent proposals have been made (see e.g. DE QUEIROZ & GAUTHIER, 1994) to modify drastically the philosophical basis of zoological nomenclature by attaching the names to "phylogenetic definitions of taxon names", that would be more in agreement with a phylogenetic system of taxonomy than other kinds of "definitions". These proposals are in my opinion based on a major misunderstanding and entertain a confusion between *taxonomy* and *nomenclature*. In the system of zoological nomenclature currently in force, allocation of zoological names to taxa is not at all based on *definitions*, *diagnoses* or *descriptions*, but on the *taxonomic allocation of name-bearing type-specimens* or *onomatophores*, which constitute an objective, material and stable connection between the real world of animal populations and the world of language, whereas definitions are liable to change (for more details, see DUBOIS & OHLER, 1997). In this system, definitions or diagnoses only contribute to the *nomenclatural availability* of names, but not to their *allocation to taxa*. On the other hand, definitions or diagnoses are crucial for the qualification of taxa, and in this domain one may well wish to use "phylogenetic definitions", but this is a matter of taxonomy, not of nomenclature. Nomenclature is a system allowing a non-ambiguous, stable, automatic and universal allocation of names to taxa, under a given taxonomy, and the current rules of nomenclature are fully compatible with any taxonomic system, including the "phylogenetic taxonomy" (or "cladonymy" sensu DUBOIS, 1997) advocated by DE QUEIROZ & GAUTHIER (1990, 1992).

Under a nomenclatural system like that suggested by DE QUEIROZ & GAUTHIER (1994), the association of a name with a given clade in a cladogram, as is the case of the name "*Rana duboisi*" in figure 3 of EMERSON & WARD's (1998) paper, could possibly be considered enough to provide a "phylogenetic definition" of this name and to make it nomenclaturally available, but this is not true under the *Code* currently in force for all zoologists. Cladograms are hypotheses of *relationships* but, although built on the basis of a character analysis, they alone do not provide the *characters* of the included taxa. Under the *Code*, the presence of a diagnosis or definition, i.e. a statement regarding *characters* (not *relationships*), is necessary for a name to be nomenclaturally available. a taxon name published only with information on the supposed cladistic relationships of this taxon is therefore not available under the present *Code*.

In conclusion, the name "*Rana duboisi*" published by EMERSON & WARD (1998) associated with a reference to the Genbank and with a position in a cladogram, but without any diagnostic character, is, according to the current *Code*, a nomen nudum.

To avoid the frequent repetition of similar nomenclatural puzzles in the future, it is highly desirable that authors try their best not to publish new names borrowed from unpublished manuscripts or from personal communications from colleagues (see e.g. DUBOIS, 1998: 20). Any name inadvertently published in such conditions may qualify, like in the present case, as a nomen nudum, i.e. a name devoid of nomenclatural status, which has no real nomenclatural consequences. But it may also happen to be a validly published name, if it was associated in its

first publication with descriptive or diagnostic data, for which e.g. paper-printed gene sequences would fully qualify. Under the *Code* currently in force, such inadvertent publication of new names associated with gene sequences would give birth to nomenclaturally available, although involuntarily so, names, aptly qualified by VENCES et al. (1999) as "phantom names". This will remain so as long as the current *Code* is in force. Seemingly, as reported by VENCES et al. (1999), the next edition of the *Code* will include the following, highly desirable, new rules, that would greatly reduce the inadvertent creation of such names: (1) the need for an explicit statement that the new name applies to a newly defined species-group taxon; (2) the need for a clear designation of a name-bearing type, deposited in an identified collection. Such rules appear very reasonable and "obvious" for all experienced taxonomists, and, once in force, they would certainly be beneficial for the future of zoological nomenclature. But it is greatly to be hoped that these rules will only be prospective (i.e., applying to works published after the new edition of the *Code*) and will have no retroactive effect. Otherwise, this might have dramatic consequences regarding nomenclatural universality and stability, as many names now considered valid by all zoologists were first published (either very long ago or more, sometimes much more, recently) without respect for these rules.

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